

THE INFLUENCE OF BAT PREDATION ON CALLING BEHAVIOR IN
NEOTROPICAL FOREST KATYDIDS (INSECTA: ORTHOPTERA:
TETTIGONIIDAE)

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1988



Frontispiece.--Spear-nosed bat, Tonatia silvicola (Phyllostomidae: Phyllostominae), from Barro Colorado Island, Panama, feeding on male katydid.

ACKNOWLEDGMENTS

This work was supported by Predoctoral Fellowships from the Smithsonian Institution, NSF (Dissertation Improvement Grant DEB-8211975), and the American Association of University Women, a Smithsonian short-term fellowship, the Florida Entomological Society, Grants-in-Aid from the National Academy of Sciences (Bache Fund), Sigma Xi, and the American Society of Mammalogists, and teaching assistantships from the University of Florida. The Smithsonian Tropical Research Institute (STRI) provided logistical support on Barro Colorado Island, Lake Gatun, Panama (BCI), and a short-term fellowship, and the Exxon Corporation funded three field assistants. Drs. J.H. Fullard and G.K. Morris (University of Toronto) flew me to Toronto on several occasions to analyze animal recordings and discuss results, they visited me in Panama, and they patiently taught me a great deal about acoustically active animals and about recording and analyzing sound. They, and Drs. C.O. Handley, Jr. (Curator of Mammals, U.S. National Museum of Natural History), and J.W. Hardy (Curator of Birds, Florida State Museum), also lent me sound recording and analyzing equipment and field gear, without which this study could not have been completed. Dr. M.D. Tuttle allowed use of his bat flight cages on BCI, and Drs. M.H. Robinson and H. Wolda

sponsored my fellowships at STRI. Glenn Morris and Dr. D.A. Nickle (Curator of Orthoptera, U.S. National Museum) helped identify the katydids.

Dr. Egbert G. Leigh, Jr., provided encouragement, valuable discussion, friendship, and moral support throughout my two year stay on BCI, as did James Fullard and Glenn Morris. (Dr. Leigh also provided limitless quantities of Bushmills.) At various times, Robin Abbey, Aixa Cabrera, Roberto Cambra, Charles Handley (and members of his BCI bat project), James Fullard, Scott Sakaluk, and Liz Stockwell worked long hard hours to help collect data in the field. Life on a small isolated island can be trying. I am particularly indebted to Dr. Lyn Loveless for her friendship and encouragement during my stay on BCI and afterwards.

Dr. Brock Fenton, my mentor from early undergraduate days, and the best teacher I ever had, deserves a special note of thanks for introducing me to the wonderful world of insectivorous bats and what they eat, as well as for his continued support, friendship and influence, through good times and bad, over the last ten years. Since entering graduate school, he and several others (Carl S. Barfield, the late Bruce Bowman, James Fullard, James E. Lloyd, Glenn Morris, Hans-Ulrich Schnitzler, and Thomas J. Walker) have greatly influenced the way I think and/or have unknowingly acted as role models. I am grateful to all of them. Last, but not least, my major professor, Tom Walker deserves a

medal for his patience in dealing with me and my comings and goings as a graduate student.

On the homefront, I am very grateful to Laurie Wilkins for being such a good friend, and a tireless sounding board throughout the last few years with respect to endeavors past, present, and future, and to my mother, Suzanne G. Belwood, for helping me out of more than one financial tight spot during my seemingly endless 'education'.

Members of my committee, Drs. T.J. Walker, J.E. Lloyd, and L.P. Brower, as well as the others mentioned in specific chapters, read and criticized this thesis, and provided help in other ways.

Acknowledgments for specific chapters are as follows:

Dr. C.O. Handley, Jr., and participants in his "BCI bat project" deserve special thanks for their help in obtaining the results that are presented in Chapters 3 and 4. R. Abbey, A. Cabrera, R. Cambra and E. Stockwell helped find bat roosts, collect insect fragments in the field, and sort them in the lab. Dr. Don Feener identified ants. Many of the ideas presented in Chapter 3 incorporate findings from other studies undertaken with M.B. Fenton (in Ontario), J.H. Fullard (in Hawaii) and H.-U. Schnitzler (in Jamaica), who are thanked for valuable discussion, some financial assistance, and the opportunity to participate in field work.

Chapter 5 is part of a larger study on the echolocation ecology of 37 species of bats on Barro Colorado Island (Belwood, Fullard and Handley, unpublished data.) The recordings presented there were made and analyzed with J. Fullard and Rita Kunz helped prepare the figures.

R.M.R. Barclay, M.B. Fenton, G.K. Morris, and J.H. Fullard read Chapter 6. Voucher specimens are housed at the Smithsonian Tropical Research Institute.

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Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

THE INFLUENCE OF BAT PREDATION ON CALLING BEHAVIOR IN
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December 1988

Chairman: Dr. Thomas J. Walker
Major Department: Entomology and Nematology

In many animals, members of one sex advertise themselves using acoustic, visual, or chemical cues in order to attract mates. These signals are usually species specific and highly localizable, which helps them function successfully in a mating context, but also means they can be used by predators. How animals resolve the conflict between attracting mates and predators is an intriguing question that has received little attention in the literature.

This study examines a predator-prey system in which acoustically orienting foliage gleaning bats (FGB) in a lowland forest on Barro Colorado Island, Panama, are attracted to the airborne songs of katydids in the subfamily Pseudophyllinae. Aspects of katydid call production that lessen predation by FGB were also studied.

During two years, field and flight cage experiments showed that members of four species of forest-dwelling FGB can use katydid songs to locate these insects as prey. A study of their echolocation calls shows that they are typical of bats that forage in cluttered environments, and probably do not allow the animals producing them to locate insects on foliage. At least one FGB, Micronycteris hirsuta, was a major katydid predator, and took insects inhabiting the forest understory that were active in the early evening when bats foraged most actively.

Airborne calling songs were recorded from members of 17 pseudophylline species sympatric with FGB. With one exception, their calls were short, sporadically produced and emphasized high audio or ultrasonic carrier frequencies. In flight cage experiments, these calls were more difficult for FGB to localize than were the longer and more frequently produced broadband calls that are typical of katydids in areas without FGB. The exception, Ischnomela pulchripennis, sang from large, spine-covered terrestrial bromeliads, which protect it from predation by FGB.

The pseudophyllines studied supplemented their short inconspicuous calls with "tremulations," substrateborne signals that travel from one individual to another through plants but are inaccessible to acoustically orienting predators like FGB. Tremulations appear to be the rule rather than the exception in tropical New World katydids

that are sympatric with FGB. They represent the first report of widespread behavioral anti-bat defenses in katydids.

CHAPTER 1 INTRODUCTION

In many animal species, members of one sex advertise themselves conspicuously using acoustic, visual, or chemical cues in order to attract mates. Well studied examples of this include the attraction of females to acoustically active conspecific male Orthoptera (grasshoppers, crickets and katydids), cicadas (Otte 1977), and frogs and toads (Kiestler 1977). Sex pheromones are chemical examples of such cues, while flash patterns (Lloyd 1977) are visual advertisements of male fireflies to the opposite sex. These cues are usually species specific, unambiguous, and highly localizable (Dumortier 1963c)-- attributes that help them function successfully in a mating context. These same characteristics, however, pinpoint the location of advertising animals to potential predators that have evolved the appropriate 'signal receiver systems'.

Information on predator response to such mating signals is limited. Lloyd (1973) lists anecdotal examples of firefly predators and parasites, but no trends are apparent with the exception of his highly specialized 'aggressive mimics' (Lloyd 1965, 1975; Lloyd and Wing 1983). Similarly, predators that exploit sex pheromones have recently been found (Harris and Todd 1980, Dixon and Payne 1980), but are

not common. Eberhard (1977) describes aggressive mimicry in a bolas spider from Colombia. Burk (1981) summarizes examples of sex-biased predation on signalling males and discusses the defenses used by some males against predators.

Examples of 'predatory phonotaxis' (Busnel 1963) are rare. In playback experiments, Kahn and Offenhauser (1949) attracted dragonflies and vertebrate predators to recordings of swarming mosquitoes, and Walker (1964) obtained similar results with katydid and cricket songs and domestic cats. Several parasitic flies, including a tachinid on crickets (Cade 1975) and mole crickets (Fowler and Kochalka 1985) and a sarcophagid on cicadas (Soper, Shewell and Tyrrell 1976), have also been found that locate hosts by their respective calling songs. The best studied example of this, however, is the discovery that fringe-lipped bats, Trachops cirrhosus (Chiroptera: Phyllostomidae: Phyllostominae), and other vertebrates in a lowland Panamanian forest prey on frogs by exploiting frog calls (Tuttle and Ryan 1981; Tuttle, Taft and Ryan 1981; Ryan, Tuttle and Taft 1981). The bats have a lowered capture success rate when frogs are not calling, they can distinguish between edible and poisonous frogs based on call type, and they choose loud and long calls over short, low intensity ones.

Recently, Tuttle, Ryan and Belwood (1985) showed that members of at least two species of 'foliage gleaning' bats in Panama, i.e., bats that pluck stationary insects from

vegetation as opposed to catching them in the air (Wilson 1973, Hill and Smith 1984), are also attracted to tape recordings of katydid calls. Katydid (Insecta: Orthoptera: Tettigoniidae) are mostly nocturnal grass-hopper-like insects and often resemble leaves. Males produce sound by moving specialized structures on their front wings against one another. When bats were presented with the recorded calls of a frog (Physalaemus pustulosus; Leptodactylidae) and a katydid (an unidentified phaneropterine with a carrier frequency of 12 kHz) simultaneously in a flight cage, Tonatia silvicola (Phyllostominae) repeatedly flew to speakers that emitted katydid songs. Under identical conditions, Trachops cirrhosus responded only to frog calls. In the absence of these, the frog-eating bats were also attracted to the katydid calls.

How animals resolve the conflict between attracting mates and predators is an intriguing question that has received little attention in the literature. In terms of basic biology, however, it has broad implications since 'advertising' for mates is ubiquitous in the animal kingdom, and there is increasing evidence that acoustically orienting predators significantly reduce the longevity of their hosts (Burk 1982). The parasitic fly Ormia lineifrons, for example, shortens the life span of male cone-headed katydids, Neoconocephalus triops, although calling and mating are not affected until shortly before death. The

larvae of the cicada parasite, Colcondamyia auditrix, mute their host soon after entering it (Soper, Shewell and Tyrrell 1976).

The phenology of calling in some Florida crickets appears to be an adaptation to avoid peak activity levels of Euphasiopteryx ochracea, a fly that is attracted to cricket calls. Seasonally, both Gryllus rubens and G. firmus are mainly silent during their fall generations, when E. ochracea are abundant. Individuals in an earlier generation, when E. ochracea are much less common, are more acoustically active (Walker personal communication). Other crickets, such as Gryllus ovisopis do not call, which is believed to be an anti-predator adaptation (Walker 1974). Seasonally, G. ovisopis adults coincide with peak activity levels of E. ochracea.

Rentz (1975) noted the conspicuous lack of calling activity in katydids in Costa Rican rain forests, i.e., in areas where foliage gleaning bats, which include the phonotactically responsive T. silvicola and Trachops cirrhosus mentioned above, are abundant. Conversely, in areas of second growth, where foliage gleaning bats are absent, he found that katydids showed greater acoustical activity. He hypothesized that reduced sound production is an anti-bat adaptation. This was also suggested by Morris (1980) and Morris and Beier (1982) to explain reduced sound production in other Costa Rican katydids.

With this in mind, the main objectives of this study were to 1) determine the extent to which foliage gleaning bats use the calls of male katydids as prey finding cues, 2) determine whether foliage gleaners are important predators of katydids (and are thus likely to represent strong selective pressures on katydid call design), and 3) determine the possible influence of bat predation on calling in katydids.

This was accomplished through field and flight cage experiments, on Barro Colorado Island, Panama (BCI), using calling insects and bats (Chap. 6), and through a survey of prey selection in the foliage gleaners (Chaps. 3 and 4). The possible influence of predation on calling behavior in katydids was determined by comparing call types of katydids in habitats with and without foliage gleaners (i.e., forests and clearings, respectively) (Chap. 6). In addition, the calls of 17 of Barro Colorado Island's forest katydids are described in detail (Chap. 7).

Most bats use echolocation (a sophisticated form of biosonar) to locate prey (Griffin 1958). The design of echolocation calls in the foliage gleaning bats of BCI was investigated to see how this differs from call design in bats that do not glean insects from foliage but take them on the wing (Chap. 5).

Chapters 3 through 7 are intended to stand on their own as papers for publication. Unavoidably, this has resulted in some duplication of text.

CHAPTER 2

STUDY SITE AND STUDY ANIMALS

All field work was conducted on Barro Colorado Island (BCI) (9°09'N, 79°52'W) between November 1982 and December 1984. BCI is an island in Lake Gatun, Republic of Panama (Fig. 2-1). It measures approximately 1500 ha and is 165 m above sea level at its highest point (Croat 1978). BCI is in the 'Tropical Moist Forest Zone' (Holdridge 1967) and is covered by semi-deciduous forest, which ranges in age from 100+ years ('young' forest) to 200 to 400 years (i.e., 'mature' forest) (Foster and Brokaw 1982). Trees in the old forest are generally larger (maximum canopy height 22 to 30 m) than trees in the young forest (maximum canopy height 18 to 24 m) and show a greater incidence of hollows and cavities. The mature forest also has the greatest number of tree falls. In addition, approximately 1% of the island consists of man-made clearings, which are dominated by weedy plants (mainly grasses, composites, and legumes) that reach a maximum height of 2 to 3 m. Herbs dominate some of the island's shoreline.

The climate is warm and humid and typical of forests in the moist lowland tropics. The average annual temperature

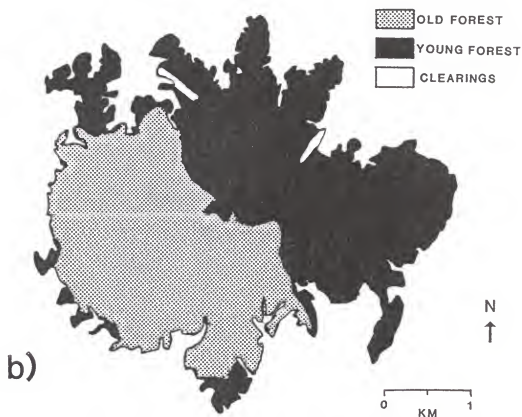
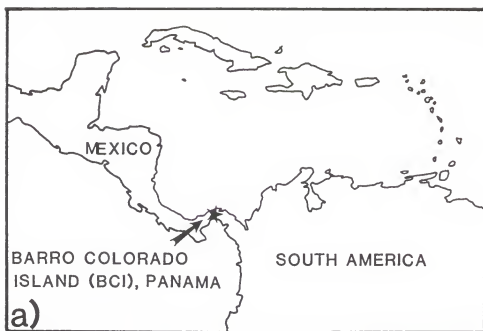


Fig. 2-1.--Location of study site (a) and detail of vegetation types (b) on Barro Colorado Island, Panama (BCI).

is 27°C and the average diurnal temperature range is 9°C. Temperatures at night typically range from 23 to 25°C.

The average yearly rainfall is about 2600 mm, 90% of which falls during the seven-month rainy season (May to December). Showers are usually short and occur in the mid to late afternoon. Rain is least likely between midnight and dawn. In its early stages, the wet season is characterized by the growth of new leaves in forest trees and by a significant increase in the number of large insects (Smythe 1982).

A three-month dry season occurs from January to March. In addition to a reduction in precipitation, trees lose their leaves, leaf litter accumulates on the forest floor, wind increases in velocity, and average relative humidity drops.

BCI supports a diverse bat fauna consisting of 58 species (C.O. Handley, Jr., personal communication). Among the non-frugivorous bats, at least 15 species [Chrotopterus auritus, Macrophyllum macrophyllum, Micronycteris brachyotis, M. hirsuta, M. megalotis, M. nicefori, M. schmidtorum, Mimon crenulatum, Phylloderma stenops, Phyllostomus discolor, P. hastatus, Tonatia bidens, T. silvicola, Trachops cirrhosus, Vampyrus spectrum (Table 2-1)] are believed to constitute a feeding guild known as the 'foliage gleaning bats' (FGB) (Wilson 1973). These include a large number of insect-eating species (Wilson

Table 2-1.--The foliage gleaning bats (Chiroptera: Phyllosotomidae: Phyllostominae) of Barro Colorado Island, Panama.

BAT	FOREARM (mm)	WEIGHT (g)
<u>Micronycteris megalotis</u>	30-34	4-6
<u>Micronycteris schmidtorum</u>	33-36	8-10
<u>Macrophyllum macrophyllum</u>	34-37	6.5-9.0
<u>Micronycteris bracyotis</u>	36-40	8-10
<u>Micronycteris nicefori</u>	37-40	8-10
<u>Micronycteris hirsuta</u>	42-45	12-15
<u>Mimon crenulatum</u>	48-52	11.5-15.0
<u>Tonatia silvicola</u>	51-53	26-32
<u>Tonatia bidens</u>	55-60	25-28
<u>Trachops cirrhosus</u>	57-61	31-35
<u>Phyllostomus discolor</u>	62-69	36-40
<u>Phylloderma stenops</u>	69-72	45-50
<u>Chrotopterus auritus</u>	75-80	65-80
<u>Phyllostomus hastatus</u>	81-85	88-105
<u>Vampyrum spectrum</u>	100+	120-150+

1973; Gardner 1977; Bonaccorso 1979; Humphrey, Bonaccorso and Zinn 1983). All belong to the family Phyllostomidae, subfamily Phyllostominae.

Unlike the more common 'aerial insectivore' bats (the Vespertilionidae, Emballonuridae, Mormoopidae, Molossidae) that feed on small flying insect prey, insectivorous FGB pluck relatively large prey from vegetation, the ground, or other surfaces and consume these at a perch (e.g., Vaughan 1976). These bats are characterized by slow maneuverable flight and have long ears (see frontispiece). They are also believed to use prey produced sounds rather than echolocation to locate food (Hill and Smith 1984). On BCI, FGB span a considerable size range (6 to 150 g) (Bonaccorso 1979), and members of at least two species, Micronycteris hirsuta (Wilson 1971) and M. megalotis (LaVal and LaVal 1980a), have been reported to eat large numbers of katydids. This makes them ideal for this study.

BCI is also home to a diverse katydid fauna consisting of at least 70 species (Belwood, personal observation). Little is known about the biology of these insects, most of which occur in forested areas rather than in clearings. Hebard (1927) provides descriptions and anecdotal observations on the biology of 81 species from Panama, including several that occur on BCI. Robinson (1969a,b) describes the defensive behaviors of orthopteroid insects from BCI, including three species of katydids. Gradwohl and

Greenberg (1982, 1984) collected arthropods, including katydids, from 'aerial leaf litter' in BCI's forest, as part of a feeding study on birds, but did not discuss katydids in detail. Walker and Greenfield (1983) and Greenfield (1983, 1988) describe calling songs and behaviors of common species that occur in grassy clearings.

Because they produce sound, katydids are appropriate candidates for 'prey' in this study. On BCI, many species in the forest understory are common where they occur and are easy to catch and observe in the lab or field. They are also easy to maintain in the laboratory and tape record using commercially available high frequency (to 40 kHz) recording equipment.

BCI was chosen as a study site because it has a rich, but manageable bat and katydid fauna, and relatively undisturbed forest. There are an elaborate trail system and modern laboratory facilities, including several large screened insectaries and a flight cage designed specifically to study bats.

More detailed information on the biology of BCI is given in Croat (1978) (flora), Leigh, Rand and Windsor (1982) (ecology and seasonal rhythms) and Bonaccorso (1979) and Handley (unpublished data) (bat ecology). Very little is known about the biology of the katydids, particularly forest species, on BCI or elsewhere in the tropics. Beier (1960, 1962) provides descriptions of over 1000 species of

New World pseudophyllines, while Morris and Beier (1982) and Morris, Klimas and Nickle (in press) discuss acoustics in katydids from Costa Rica and Ecuador, respectively. A considerable literature exists on the function of mating sounds and on the biology of the insects producing them (e.g., Alexander 1960, 1961; Dumortier 1963a,b,c; Huber 1963; Sales and Pye 1974; Otte 1977; Gwynne and Morris 1983; Kalmring and Elsner 1985).

Chapter 3
DIET DETERMINATION IN INSECTIVOROUS BATS, WITH SPECIAL
REFERENCE TO THE NEW WORLD FOLIAGE GLEANERS

Introduction

With nearly 900 species, bats constitute the second largest order in the class Mammalia and nearly one-quarter of all mammal species (Nowak and Paradiso 1983). While these animals are known to be important predators of insects in terms of biomass consumed (e.g., Constantine 1970, Gould 1970, Bateman and Vaughan 1974), relatively little is known with respect to what most bats eat (Yalden and Morris 1975, Gardner 1977). This is especially true in the tropics, where bats represent nearly half of all terrestrial mammals (Nowak and Paradiso 1983), and many species are sympatric and in the same feeding guilds (e.g., Wilson 1973, Gardner 1977, Bonaccorso 1979).

Precise information on the prey taken by bats is important for, among other things, ecological studies dealing with faunal (community) structure (e.g., Tamsitt 1967; McNab 1971; Fenton 1972; Fleming, Hooper and Wilson 1972; Wilson 1973; Black 1974; Findley 1976; Belwood 1979; Belwood, Fullard and Handley in preparation), functional (jaw and wing) morphology (e.g., Mortensen 1977; Belwood 1979;

Freeman 1981a,b, 1984, 1988; Reduker 1983; Norberg and Rayner 1987), the effects of bat predation on the development of defenses in major insect groups (Roeder 1967; Miller and Olesen 1979; Moiseff, Pollack and Hoy 1978; Yager and Hoy 1986; Belwood this study, Chaps. 6 and 7), and for comparative studies on the adaptive significance of echolocation call design (e.g., Simmons, Fenton and O'Farrell 1979; Fenton 1982b; Neuweiler 1984; Neuweiler, Singh and Sripathi 1984; Barclay 1988; Belwood, this study, Chap. 5; Belwood, Fullard and Handley, in preparation). With respect to the latter, Pteronotus parnellii (Mormoopidae), for example, is the best studied bat with respect to echolocation [see papers in Nachtigall (1988)], but its natural foraging behavior and diet have only recently been studied (Schnitzler et al., in preparation; Belwood and Schnitzler, in preparation).

Stomach content- and feces-analysis are the most common methods used to determine diet in insectivorous bats (Whitaker 1988). Although biases are associated with these techniques (Rabinowitz and Tuttle 1982, Kunz and Whitaker 1983, Whitaker 1988), they can give an accurate picture of prey selected by some of the insect eaters. This is particularly true with respect to the 'aerial insectivores', which in general are worldwide in distribution and represent about 70% of all bat species (Wilson 1973). These bats catch and eat relatively small insects whole and on the

wing. In contrast, the insectivorous 'gleaning' and 'flycatching' bats, which are less common, mainly tropical, and less well studied, feed on relatively large, often non-flying insects (Wilson 1973, Kunz 1982, Hill and Smith 1984:62). These are plucked from vegetation, the ground, or other substrates (in the gleaners--e.g., Phyllostomidae: Phyllostominae, some Nycteridae, some Megadermatidae), or from the air [in the flycatchers; e.g., Rhinolophidae (including Hipposideridae); some Megadermatidae, some Nycteridae]. The insects captured are usually consumed from a woody perch at a feeding roost where their wings, legs and heads are culled prior to ingestion (e.g., Fenton 1975:5-6; Vaughan 1976, 1977; O'Shea and Vaughan 1977; LaVal and LaVal 1980^{a,b}; Schnitzler et al. 1985; Vaughan and Vaughan 1986; Marimuthu and Neuweiler 1987).

Two implications arise from this for diet determination studies. First, stomach content and fecal analyses may not accurately reveal diet because most taxonomically important insect parts are discarded (e.g., Ross 1967:211). This is particularly important when large insects with long wings and long legs (e.g., katydids) are consumed, because these body parts are always discarded. Second, diet may best be determined by examining culled insect pieces, if these can be found.

Recently, the diets of neotropical insectivorous foliage gleaning bats (FGB) (Phyllostomidae: Phyllostominae) have been described using both stomach and fecal analysis (Whitaker and Findley 1980; Humphrey, Bonaccorso and Zinn 1983; Howell and Burch 1974) as well as roost cullings (Wilson 1971, LaVal and LaVal 1980a). The results of these studies differ despite the fact that materials from the same species were examined. Using fecal analyses for example, Humphrey, Bonaccorso and Zinn (1983) concluded that FGB in Panama comprised a 'beetle-eating guild'. Conversely, Wilson (1971) and LaVal and LaVal (1980a), who examined two of the same bat species, Micronycteris hirsuta and M. megalotis respectively, concluded that although beetles are important in the diets of these bats, Orthoptera (katydids and roaches) were the dietary staples. Belwood (Chap. 4) observed that beetles occur in the diets, but that Orthoptera appeared to be the most important components, especially in terms of biomass. LaVal and LaVal (1980b) noted similar differences between the results of their and other (Chapman 1958, Fenton 1975) studies of feeding in the African Nycteris thebaica (Nycteridae) using roost cullings, and studies based on stomach or feces contents (Whitaker and Black 1976; Fenton et al. 1977). Similarly, the results of feeding studies on Antrozous pallidus (Vespertilionidae), a gleaner in the southwestern U.S.A., differ as a function of the technique used to determine diet. Using roost cullings,

Ross (1967:235) and O'Shea and Vaughan (1977) listed insects belonging to more than six orders (comprising 20 families and 54 species) as prey items, whereas Whitaker, Maser and Keller (1977) listed members of only four orders and seven families (and no species) as prey when stomach contents were used to analyze prey taken.

In view of these discrepancies, and the growing interest in bat diets, especially in the tropics, the purpose of this paper is to review methods of diet determination in insectivorous bats, outline new and old techniques not adequately covered in previous reviews, especially with respect to foliage gleaning bats (e.g., Whitaker 1988), and establish the least biased way to study feeding habits in this group. While this is mainly concerned with insectivorous gleaners, carnivorous gleaners, flycatching species, and the aerial insectivores will also be considered where appropriate. Some previously unpublished information is largely from a two year study on the feeding and foraging ecology of insectivorous FGB (Phyllostomidae: Phyllostominae) on Barro Colorado Island, Lake Gatun, Panama (BCI) (9°09'N, 79°51'W), some details of which are presented in Chapter 4.

Habitat Use and Foraging Activity Patterns

Insects (i.e., potential available prey) vary in both time and space. Therefore, before one can accurately determine diet in insectivorous bats, it is important to

know both when and where the bats to be studied forage (Fenton 1982a). This allows insect resources to be sampled (Kunz 1988) at the appropriate times and places such that prey available to bats can be compared to prey eaten. In some cases it may also be necessary to know what other bats forage in a given area as members of one bat species have been shown to forage on different insects depending on what other bat species are present (e.g., Husar 1976).

The use of Japanese mist nets and Tuttle traps (Tuttle 1974, Tideman and Woodside 1978) placed at bat day roosts allows the beginning and end of foraging activity to be monitored (e.g., Kunz 1974; Schnitzler et al. in preparation) and identifies when bats forage in the field (Kunz 1973; Handley--Barro Colorado Island bat project, unpublished data). In roosts containing only one or two species, visual (e.g., Swift and Racey 1983) or acoustic censuses [using devices sensitive to ultrasonic echolocation calls, e.g., Fenton (1970)] also allow flight behavior and activity to be quantified with the added benefit of minimizing disturbance to the bats. Most bats have two to three feeding bouts per night. Activity in night roosts (roosts other than the principal diurnal resting place that are used at night between feeding bouts) can also be monitored directly using a variety of methods (Erkert 1982:202) including temperature probes to record the presence or absence of bats (Kunz 1974).

Using these techniques, temporal activity patterns have been found to vary among species (e.g., Kunz 1973, Swift and Racey 1983), among conspecifics as a function of reproductive condition [especially in females, e.g., Swift (1980)] or age [adult vs. juvenile--Kunz (1974)], and as a result of atmospheric conditions [particularly rainfall, temperature and moonlight; e.g., Kunz (1974)]. Foraging style may also affect temporal aspects of emergence from roosts and foraging.

Gleaning bats appear to begin to forage longer after sunset than do the aerial insectivores. This has been noted in Antrozous pallidus (O'Shea and Vaughan 1977), Macrotus waterhousii (Phyllostominae) (Belwood this study, unpublished data), M. californicus (Vaughan 1959:36) and the North American plecotines (Vespertilionidae; Barbour and Davis 1969). O'Shea and Vaughan (1977) suggest that this may be an attempt to avoid visually orienting predators, because FGB are relatively slow fliers and often land on the ground to capture prey. However, Micronycteris hirsuta in Panama have been observed to leave their roosts about 15 min before it was too dark to see in the forest without the help of a flashlight (Belwood this study, Chap. 4).

In general, determining where bats forage can be difficult because members of most species forage at night when it is dark and are thus difficult to see. Also, members of many species roost in large concentrations that

necessitate flights of great distances (up to 100 km) to unknown feeding grounds [e.g., Tadarida brasiliensis (Molossidae) in Texas (Davis, Herreid and Short 1962; Williams, Ireland, and Williams 1973) and Pteronotus parnellii in Mexico (Bateman and Vaughan 1974) and Jamaica (Schnitzler et al., in preparation)]. Most areas contain more than one bat species and many that belong to the same feeding 'guilds' (sensu Root 1967; Wilson 1973, Bonaccorso 1979, Fenton 1982b). This increases problems in the identification of the bats under observation (e.g., Shields and Bildstein 1979). Only rarely are single-species situations found (e.g., Belwood and Fullard 1984), or exceptional situations that allow individual species to be identified as they forage (e.g., Greenhall 1966; Jeanne 1970; Norberg 1976; Woodsworth, Bell and Fenton 1981).

Several recently commercially available devices can aid in the precise identification of foraging bats in the field. Ultrasonic detectors (Simmons et al. 1979) tuned to species-specific echolocation call frequencies allow bats to be identified in both natural feeding grounds (e.g., Buchler 1976b; Andersen and Miller 1977; Fenton and Thomas 1980; Schnitzler et al. 1985) and at insect concentrations at lights (Bell 1980, Belwood and Fullard 1984, Haffner and Stutz 1986). 'Search phase' calls (sensu Simmons, Fenton and O'Farrell 1979) are usually monitored, although the entire call sequence that occurs during insect pursuit

[search, approach, and terminal feeding buzzes (ibid.)] can also be heard. In addition, an ultrasonic microphone - coupled to a zero-crossing period meter (Simmons et al. 1979) allows echolocation calls to be displayed on a portable oscilloscope for use in the field (e.g., Fenton, et al. 1980; Bell 1980).

Use of these techniques is limited to species whose echolocation calls are known, or can be determined in the laboratory or field prior to field studies (e.g., Fenton 1982b). Intraspecific geographic variation in echolocation call parameters occurs in some species (Thomas, Bell and Fenton 1987) and this should be considered in all studies that use data obtained with ultrasound detectors. Unfortunately, such data are biased for high intensity echolocators (e.g., Bell 1980). "Whispering bats" (Griffin 1958:247, Novick 1977:169), which include most of the gleaners and some of the frugivores, are characterized by low intensity, high frequency, and directional echolocation calls that usually cannot be detected (e.g., Fenton and Bell 1981). In these cases, radio-telemetry can be used to determine foraging patterns (Morrison 1978a,b; Williams and Williams 1967; Vehrencamp, Stiles and Bradbury 1977). Some bats such as Euderma maculatum (Vespertilionidae) have audible (< 20 kHz) echolocation calls and ultrasound detectors are not necessary to monitor their calls.

Aluminium or plastic bat bands, affixed to the forearm, have a long history of use in identifying individual bats for large scale banding studies (e.g., LaVal 1970, Keen and Hitchcock 1980). Plastic arm bands applied in different color combinations can also be used, in conjunction with spotting scopes or binoculars, to identify individuals foraging in the field (e.g., Vaughan and Vaughan 1986) as well as the habitats used by these bats. Bands covered with reflective tape in different colors can be used to distinguish between species (Swift and Racey 1983; Fenton, et al. 1980), sexes, age groups (Racey and Swift 1985), or individuals (Rydell 1986), all of which can forage differently.

As pointed out by Buchler (1976a), reflective bands are "passive" tags (energy reflectors), and the bats carrying them must be located in the field with the aid of flashlights (Bradbury and Vehrencamp 1976a), chemiluminescent tags (see below) or ultrasound detectors (Racey and Swift 1985) before they can be followed. The bands have the advantage, however, of allowing marked individuals to be observed over long periods (e.g., an entire feeding season) such that changes in individual foraging behavior (e.g., habitat used, distance covered) can be observed. This is important, because seasonal changes in insect availability (e.g., Vaughan and Vaughan 1986) and reproductive condition

(e.g., Racey and Swift 1985) are known to alter foraging patterns.

Most successful bat banding studies (and those involving the use of reflective tape) have taken place in temperate areas. In the humid tropics, and during the course of a ten year banding study of bats in lowland Panama, Handley (personal communication) observed that 'standard' (forearm) bands can cause severe arm infections. Therefore, their use is not recommended in the tropics. Instead, Handley (*ibid.*) recommends 'collaring' bats with small numbered aluminum bands that are placed around the neck on a beaded, stainless steel chain. Unfortunately, it is doubtful that reflective tape would be visible to an observer if placed on such a necklace.

In contrast to the passive tags, chemiluminescent (light) tags (Buchler 1976a) are "active" (energy emitters) and allow continuous observation of bats for relatively long distances over a period of several minutes to several hours (the 'life' of the tag) (Buchler 1976a; Fenton, Bell and Thomas 1980; Fenton et al. 1980; Fenton, Thomas and Sasseen 1981; Bell 1980; Racey and Swift 1985; Caire et al. 1984; Schnitzler et al., in preparation). These can also be used with ultrasound detectors to quantify prey captures by counting feeding buzzes in particular individuals (e.g., Racey and Swift 1985; Schnitzler et al., in prep.)). Unfortunately, in some cases light tags may be difficult to

distinguish from luminescent insects such as the light producing click beetles that are plentiful in many tropical areas (Belwood, personal observation). They are also difficult to see on bats that forage in heavily forested areas.

Feeding Behavior

Direct Field Observations

Bats that begin to forage early in the evening [e.g., some Emballonuridae (Bradbury and Vehrencamp 1976:368)] or before dark [e.g., E. maculatum (Woodsworth, Bell and Fenton 1981; P. parnellii (Bateman and Vaughan 1974))] can be observed directly against the darkening night sky until they are no longer visible. This has yielded a considerable amount of information on bat feeding behavior.

Traditionally, for example, E. maculatum have been classified as "gleaners" simply because they have the long ears characteristic of bats with this foraging style (Wilson 1973:25). Recent direct observations, however, reveal that they are actually "aerial insectivores" (Woodsworth, Bell and Fenton 1981).

Spotting scopes and infrared and other night viewing devices also allow individuals to be observed in all phases of foraging activity, from when they exit roosts (e.g., Swift and Racey 1983) to how they forage at close range, naturally and undisturbed in the field. Vaughan (1976,

1977) and Vaughan and Vaughan (1986) used these devices to describe feeding and foraging behavior in three African foliage gleaners or flycatching bats, Cardioderma cor, Lavia frons (both Megadermatidae), and Hipposideros commersoni (Rhinolophidae: Hipposiderinae). These observations confirm the differences in foraging technique among aerial insectivores, gleaners, and flycatchers.

Compared to aerial insectivores, FGB and flycatching bats are remarkably sedentary. H. commersoni, for example, spend less than five percent of their foraging time on the wing (Vaughan 1977). Similarly, C. cor sally out after prey in flights that usually last less than five s and cover less than 25 m (Vaughan 1976). Flying is the most energetically costly mode of transportation (Schmidt-Nielsen 1972), and this is particularly true for gleaners and flycatchers, all of which have broad wings and are relatively inefficient long distance fliers (Mortensen 1977, Norberg and Rayner 1987). Yet, the energy expended by these bats per prey item captured is relatively low.

Vaughan's observations reveal that foraging in the gleaners and flycatchers is highly stereotyped. These bats usually hang upside down from woody perches close to the ground and scan their immediate surroundings by rotating their bodies and moving their pinnae back and forth until they perceive potential prey. In H. commersoni this appears to be done using echolocation for prey that are captured in

the air, while C. cor listen for the sounds of insects that are captured on the ground. Hearing in the latter is acute as they appear able to distinguish between the sounds of prey and nonprey items. To some extent, all these bats include flycatching and gleaning in their foraging repertoires.

In all cases, Vaughan's bats captured relatively large insects and returned with them to their original perches on tree limbs to feed. Hard portions of their prey were culled and accumulated in large numbers beneath the feeding bats because the same few perches were used over and over again by the same individuals.

Similarly, Neuweiler et al. (1985) and Schnitzler, Hackbarth et al. (1985) used direct observations to study Rhinolophus rouxi (Rhinolophidae), another flycatcher/gleaner that forages in dense vegetation in Sri Lanka. These bats foraged in one of two ways depending on time of night. In early evening, they hunted on the wing close to and within vegetation. Later in the evening, they perched from tree limbs and used echolocation to catch flying prey. Presumably, these changes in foraging strategy reflected hourly differences in insect availability, although no data were collected to test this. These observations and those of Vaughan (above) show that gleaning and flycatching may not be very distinct, and that bats are flexible in their foraging styles and choice of prey and

should be observed carefully and for long periods of time before they are assigned to feeding guilds.

That changes occur in foraging behavior as a result of larger scale (seasonal) changes in insect availability has also been shown by direct observation of individually foraging bats. O'Shea and Vaughan (1977) showed that A. pallidus decrease foraging activity during cool weather when insects are scarce. Similarly, C. cor change from ground foraging to flycatching (Vaughan 1976), and L. frons change the frequency and duration of their foraging flights as a function of seasonal ground cover and insect availability (Vaughan and Vaughan 1986).

Tuttle and Ryan (1981, 1982), Ryan, Tuttle and Taft (1981) and Ryan, Tuttle and Rand (1982) used a night vision scope to observe Trachops cirrhosus, a carnivorous phyllostomine FGB, respond to advertisement songs as feeding cues to locate frogs in natural ponds in Panama. Using this device, Ryan, Tuttle and Taft (1982) documented several aspects of bat-frog interactions, including evasive responses in the frogs (Tuttle, Taft and Ryan 1982) and predation risk as a function of chorus size. In apparent contrast to this, Ryan and Tuttle (1987) used a night vision scope to show that C. cor in Kenya do not use frog calls as prey finding cues although they do feed on frogs.

Night vision scopes have also been used successfully to observe aerial insectivore bats as they feed. P. parnellii,

for example, were observed as they foraged in their natural habitats in Jamaica (Schnitzler et al. in preparation). The highly specialized constant frequency echolocation signals of these bats are believed to allow these bats to hunt flying insects amidst a background of dense foliage (Schnitzler 1987). This was confirmed using a night vision device, alone, and coupled to video and audio recording equipment.

Semi-natural foraging situations can also be created in the field to lure bats to a particular area to photograph and tape record them as they feed. Approaches of the bats to 'glint machines' (devices that simulate acoustic 'glints'--the rhythmic changes in echo frequency and amplitude produced by flying insects) were observed using night vision scopes and were later documented with a multi-flash still camera (Schnitzler et al., in preparation). Multi-exposure photography, synchronized with high speed tape recordings, can also be used to document echolocation and prey capture in aerial feeding bats in the field (Schnitzler et al. 1987; Schnitzler et al. in preparation).

Similarly, ultraviolet lights can be set up in the field to lure swarms of insects that in turn attract large numbers of insect eating bats that can be studied. For example, Fenton and Morris (1976) used lights and tape recorded calls of foraging bats to examine opportunistic

feeding, while Bell (1980) used similar techniques to study habitat use and bat responses to insect patches. Bell and Fenton (1984) also used this technique to determine the type and size of prey caught by Hipposideros ruber.

Indirect Field Observations

Many FGB fly from foraging areas to feeding roosts with large insects or other prey items in their mouths, which if captured with a bat can usually be identified to help determine feeding strategy. In Panama, Bonaccorso (1979) caught Tonatia bidens (Phyllostominae) carrying a cicada (Homoptera: Cicadidae: Fidicina mannifera), and Belwood (this study) caught T. bidens and T. cirrhosus with insects [one large roach (Periplaneta sp.), one large male cicada (F. mannifera)] and insects (a female pseudophylline katydid, Docidocercus gigliotosi) and a frog Centrolenella sp. (Centrolenidae), respectively. These prey are mainly ground or foliage dwelling and indicate a foliage gleaning foraging style at least during part of the bats' foraging periods. The carnivorous phyllostomine Chrotopterus auritus has been netted with decapitated doves, indicating that it includes birds in its diet (Peracchi and Albuquerque 1976). This technique can also be used with aerial insectivores; Belwood (unpublished data) recently caught a P. parnellii in a mist net in Jamaica with a cricket leg (Gryllus sp.; Gryllidae) in its mouth.

Determining how much individuals have eaten also yields important information with respect to diet, and can easily be done by taking pre- and post-feeding weights of bats (Kunz 1974, Anthony and Kunz 1977). Using this method, comparisons in food consumption can be made between bats of different sexes, bats caught early and late in the evening (i.e., during the first and subsequent nightly foraging bouts--when insect populations are likely to be different); simultaneously among non-reproductive, pregnant or lactating females, and on animals of different age classes that occur at the same site. Comparative estimates of caloric intake can also be made from animals in all of these groups using simple formulae based on wet weights of food consumed or fecal dry weights (Kunz et al. personal observation as cited in Anthony and Kunz 1977:778).

Laboratory Observations

Gleaning Bats

Because they are more or less sedentary and feed on relatively large insects, FGB are fairly easy to keep in the laboratory. Notable exceptions include small bodied animals [e.g. Micronycteris megalotis, M. schmidtorum (Phyllostomidae); Belwood, unpublished data] and larger species that just do not do well in captivity (e.g., Nycteris spp.; M.B. Fenton, personal communication). In all cases, laboratory observations should be made during the bats'

normal active periods, as some have a tendency to enter torpor if they are not fed at the appropriate times (Belwood, personal observation).

Laboratory observations can be used to confirm or expand field observations. Tuttle and Ryan (1981), for example, elicited predatory responses in wild caught and untrained T. cirrhosus to recorded frog calls in a large (4.5 by 4.5 by 2.3 m) screened flight cage in Panama. In 'choice' experiments, they described and quantified bat responses to different frog calls. In the same flight cage, Belwood (this study, Chap. 6) attracted wild T. silvicola to the calls of live singing male katydids and Tuttle, Ryan and Belwood (1985) showed that T. silvicola and T. cirrhosus, which are sympatric and similar in size, morphology, and foraging behavior, respond phonotactically only to the calls of their preferred prey (insects or frogs, respectively) when these are presented simultaneously. Similarly, Fiedler (1979) and Marimuthu and Neuweiler (1987) observed the carnivorous Old World FGB Megaderma lyra (Megadermatidae) capture small vertebrates in the laboratory using prey-produced sounds rather than echolocation. [Even in the laboratory, these bats had favorite feeding perches from which they sallied out after prey, as has been observed in other FGB in the field (Vaughan 1976, 1977; Schnitzler et al. 1985; Vaughan and Vaughan 1986).] Others, [Barclay, et al. (1981); Ryan, Tuttle and Barclay (1983), Bell (1985);

Bell and Fenton 1986; and Belwood (this study, Chap. 5)] have used laboratory studies to study the sensory cues used by FGB to locate their prey.

Prey handling and processing, as well as prey preferences, can be studied and compared in the lab, and much can be learned from these observations. Fenton, Gaudet and Leonard (1983) observed two African gleaners (Nycteridae), Nycteris grandis, a 35 g omnivore, and N. thebaica, a smaller insectivore, feed in the lab. They found that both species searched for prey from a perch, and that prey were always consumed at a perch, as occurs in the field (Fenton, Thomas and Sasseen 1981). Prey were captured from surfaces or from the air, and N. grandis readily accepted small vertebrates and insects. It ate small frogs whole, but left behind the legs of larger frogs and the wings and fur of bats fed to it. N. thebaica fed on insects, whose legs and wings were culled prior to ingestion. (These findings are important to consider with future fecal or stomach content analyses.) Katydid were the preferred insect food items for both species, and moths were the least preferred, indicating that the bats distinguished between different kinds of insects. These findings may explain why LaVal and LaVal 1980b) found relatively few moths eaten by N. thebaica in the field.

Nycteris responded to prey produced sounds, but also produced echolocation calls during prey capture. This and

other studies indicate that as a whole, FGB worldwide use a variety of senses (echolocation, vision, prey produced sounds) to locate their prey, the relative importances of which depend on species. Still unknown, is the extent to which echolocation alone can be used to localize prey. Many studies indicate that echolocation is not sufficient to capture prey (Ryan and Tuttle 1987; Marimuthu and Neuweiler 1987; Belwood this study, Chaps. 5 and 6), but see Bell (1985).

Prey handling in New World FGB is similar to that described for Old World species. Howell and Burch (1974), Greenhall (1968), and Constantine (1966) observed feeding in large captive carnivorous phyllostomines (Vampyrum spectrum and C. auritus), and Belwood (this study, Chap. 4) observed the same in many of the insectivores in this subfamily. In these studies, how much the bats consumed, what food items were refused (e.g., fruit), and the degree to which prey were culled could all be determined.

Aerial Insectivore Bats

Aerial insectivore bats will also fly and forage for insects in a flight cage providing it is large enough (Goldman and Henson 1977; Schnitzler et al., in preparation). Such observations are potentially very useful as aerial insectivores cannot usually be observed at close range in the field. In the recent study on foraging in P.

parnellii (Schnitzler et al. in preparation), these bats were allowed to fly and feed freely in a small (3 by 3.5 by 2.5 m) screen flight cage, where their foraging behavior and echolocation were recorded photographically and acoustically. These bats only went after flying insects and fed almost entirely on the wing. Only occasionally did they land on the cage's surface during a feeding bout. Like their foliage gleaning counterparts, they culled wings, legs and other taxonomically important pieces of their prey, but they did so on the wing. Culled insect pieces fell to the ground and could be retrieved (Belwood and Schnitzler, in preparation). The culling of prey in flight has also been observed in the field in at least one other aerial insectivore, Lasiurus cinereus semotus in Hawaii (Belwood and Fullard 1984), and has important implications for diet determination in these bats if fecal and gut content analyses are used since prey are usually identified by head and wing elements (Whitaker 1988).

Fecal and Stomach Content Analyses

Fecal- and stomach-analyses have been used to determine diet in FGB, hawking species and aerial insectivore bats in both the Old and New Worlds. For fecal analyses, bats are captured in the field (Tuttle 1976), identified to species, sexed, aged (as a function of degree of closure and ossification of phalangeal epiphyses--Barbour and Davis

1969), and weighed. They are retained singly in containers, preferably clean cotton bags, while they defecate. Food passes through a bat's digestive tract in one to two hours (Buchler 1975). The above-mentioned statistics should always be noted as age, sex, and reproductive condition can all affect prey selection and other aspects of foraging behavior.

Because bats chew their food into tiny pieces, reconstructing the last meal eaten using fecal or stomach contents is difficult. This is easier to do if a reference collection representing the insects in a bat's foraging area is available. Therefore, the more one knows about where and how bats forage, the better.

Kunz (1974) for example compared dietary intake in different age, sex, and reproductive classes of Myotis velifer (Vespertilionidae). Compared to non-reproductives, females in the last stages of pregnancy ate the least (a function of reduced stomach capacity and decreased maneuverability) and lactating females ate the most (in response to the increased energy requirements of milk production). In spite of this, there were no qualitative differences in diet. In contrast, Belwood and Fenton (1976), found that lactating female M. lucifugus in southeastern Ontario had diets that differed significantly from those of non-reproductive females and males. The former fed selectively on moths, while their non-lactating

counterparts ate prey (mainly chironomid flies) in the proportions in which they were available. Possible, but untested, hypotheses (Belwood 1976) to explain the latter include the use of foraging ranges that were closer to maternity roosts, later exit flights from roosts, or active selection for moths to increase the acquisition of nutrients necessary for the growth of young.

The age of the foraging bats can also affect prey selection. There is evidence, for example, that juveniles are less efficient and less selective fliers than adults (Belwood and Fenton 1976, Anthony and Kunz 1977). Also, older bats and banded individuals (who chew their bands) show greater tooth wear than do younger ones, and this may affect the selection of prey (Belwood, personal observation).

It is also important to note time of evening that fecal samples and gut contents were collected, as there are taxon-specific differences in the nightly abundance and diversity of insects (Williams 1935, 1939; Wellington 1945). Because they feed several times per night, bats that forage early in the evening are exposed to an insect fauna that is different from that occurring later in the evening. In some areas insects are most available before midnight and bats respond by eating the most at this time (Anthony and Kunz 1977).

Bats with full stomachs can be caught within one to two hours, or less, after foraging has begun (Anthony and Kunz 1977; Belwood and Schnitzler, in preparation; Belwood this study, Chap. 4). Because food passes through a bat's digestive tract quickly (Buchler 1975) the bats whose feeding habits are to be sampled must be processed quickly. To collect feces, bats should be retained individually for several hours in clean bags and then released.

If bats are collected for stomach content analysis, only those that have recently fed should be captured. These can be distinguished by greatly extended abdomens.

(Pregnant bats can be mistaken for bats that have recently fed, but large embryos in the lower abdomen can usually be differentiated from a food bolus by a harder feel.) Bats emerging from day roosts, or those captured in the field shortly after dark before they have had a chance to feed, should not be collected. While this may seem obvious, it is not uncommon to find reports in the literature of unfed bats that have been collected for their stomachs (e.g., Easterla and Whitaker 1972; Whitaker and Black 1976; Whitaker, Maser and Keller 1977; Vestjens and Hall 1977).

If stomachs are to be taken, the bats must be killed immediately in order to prevent digestion of food materials. Whitaker (1988) describes methods to quantify prey in the gut or feces, and he, Rabinowitz and Tuttle (1982) and Kunz and Whitaker (1983) describe the biases that

are associated with fecal analysis. Briefly, these concern the differential digestion of hard and soft insects and the resulting over- and under-representation, respectively, of these groups. Because many feeding studies compare prey available to prey selected, it should also be noted that most insect-trapping methods are biased (Southwood 1966).

Bats that have recently fed produce a large number of fecal pellets, the dry weight of which can be used to calculate food consumed (Anthony and Kunz 1977). For example, 125 P. parnellii, captured returning to cave roosts in Jamaica immediately after feeding, produced an average of 25.6 ± 9.5 pellets (range = 9 to 63), Belwood and Schnitzler, in preparation), and the average number of pellets produced by Panamanian FGB was 29.9 ± 9.6 (Belwood this study, Chap. 4). Similarly, a recently fed Myotis grisescens studied by Rabinowitz and Tuttle (1982) produced 33 pellets after just one feeding bout. These results are important because feeding studies have been based on as few as 2 to 4 pellets per animal (e.g., Humphrey, Bonaccorso and Zinn 1983). Such small samples do not give an accurate representation of bat diets, but have been used to determine resource partitioning and community and guild structure (*ibid.*). It is also noteworthy that many bats defecate while they fly (see above); therefore all the insects ingested in the feeding bout prior to capture may not be represented. Also, pregnant bats produce fewer fecal

pellets than do non-reproductives because their food intake is lower (Kunz 1974).

Under special circumstances, as in large single-species maternity colonies where it can be ascertained that members of only one species and sex inhabit an area, fecal material can be collected from the floor of the roost (Belwood 1976; Fenton, Thomas and Sasseen 1981; Swift and Racey 1983), or from structures (e.g., walls) surrounding roost entrances (Belwood 1976). Large samples can be collected in this way.

Regardless of how they are collected, fecal samples should be oven dried for several hours to prevent molding and they should be stored and labelled in small paper envelopes instead of in moisture retaining vials or plastic bags. Samples from individual bats should be kept separate and stored with an insect deterrent [e.g., naphthalene or paradichlorobenzene (PDB)]. Scats should be examined using a dissecting microscope. They should be placed in a petri dish containing alcohol and teased apart one by one, which helps keep all the parts from one insect together. Whitaker (1988) discusses methods to quantify and identify the prey eaten. If body parts (wings, legs, heads) cannot be identified, they can at least be measured in order to determine the approximate size of the insect consumed.

As a group, moths appear to be one of the most important prey items in bat diets. Thus, in some studies it may be important to determine the importance of these

insects in bat diets. This can be done easily using a technique devised by Black (1972, 1974), in which the number of moth scales per unit area in a gram of dried feces is determined. As pointed out by Whitaker (1988) these results are relative and cannot be used to determine the actual number of moths eaten.

Culled Insect Fragments

In areas where FGB are common, culled prey fragments can be found in roosts or beneath areas used for feeding. Roosts include tree holes and hollows, caves, man-made structures, spaces under fallen trees, the inside of large termite nests, and in tree canopies among leaves (Kunz 1988). These roosts often occur close to the ground and are easy to find where bats are numerous. They can be identified by the presence of bats, prey cullings, or both. Because many of the bats are colonial and use the same roosts over and over again, the remains of several hundred insects can accumulate in a few days (Wilson 1971; LaVal and LaVal 1980a,b; Fenton, Thomas and Sasseen 1981; Belwood this study, Fig. 3-1.).

Insect remains should be removed directly from these roosts with a small trowel, and can be transported in large, labelled plastic bags. Gloves should be worn when removing cullings and surrounding leaf litter or soils, as stinging ants (e.g., Paraponera spp), termites and scorpions may also



Fig. 3-1.--Insect remains in one roost of the foliage gleaning bat Micronycteris hirsuta (Phyllostomidae: Phyllostominae) on Barro Colorado Island.

be present. Care should be taken to avoid the venomous snakes that may be present near bat roosts in some geographic areas. This is especially true when roosts are in hollow trees. The cullings should be dried in a cool oven ($< 100^{\circ}\text{C}$) in large trays for 24 h to prevent molding and to kill small invertebrates (mites, roach nymphs, ants) that are also collected. They should be stored in a dry place with PDB.

Insect forewings are the most common and taxonomically useful prey items that occur in the roost cullings, and these can be separated from the oven-dried substrate with forceps. The wings should be removed one by one and placed in piles with other pieces that are identical in size, shape, color, and pattern. They are then grouped in pairs (i.e., a left and right wing), each of which, along with the remaining single, unmatched wings, is counted as one insect eaten (see Dunkle and Belwood 1982). The wings are then identified by comparing them to wings or whole insects in a reference collection that has been made from insects in the study area or standard texts with good drawings (e.g., CSIRO 1970). Identification can usually be made to 'species' in common forms, or to 'morphotype' in cases where insects are poorly known. In tropical areas, many of the insects eaten may belong to unidentified species, in which case specimens (preferably the entire insect--not parts) should be sent to the appropriate source for taxonomic classification.

Sex biases in prey captured can indicate specialized foraging methods, such as phonotactic responses to insect sound (Tuttle, Ryan and Belwood 1985; Belwood this study, Chap. 6). Male cricket and katydid wings can be distinguished by their sound producing organs (Fig. 3-2; e.g., Borror and Delong 1971). In some cicadas and beetles, male wings are more brightly coloured or smaller, respectively, than those of females. Again, these generalizations should be confirmed by making a good reference collection. Ovipositors from female crickets, katydids and cicadas (Fig. 3-3) can occur in large numbers (this study), and in some cases without accompanying wings. Unless one has a search image for these, they can easily be overlooked.

It is possible that flightless insects and other arthropods may be eaten by bats and can go undetected unless portions of their bodies are found. In some studies (Belwood this study, Chap. 4) spiders, for example, have been recognized by their legs, and caterpillars by their head capsules. Unfortunately, insect legs are not often easy to identify taxonomically.

Relative biomass values of prey taxa can easily be estimated using prey remains found at bat roosts. First, several individuals of each taxon eaten (and sex, if these differ in size) should be weighed (without their heads, legs and wings) to obtain average weights (e.g., Appendix).



Fig. 3-2.--Front dorsal view of the wings of a male katydid (a), and ventral surface of the basal portion of the left front wing showing the file (b).

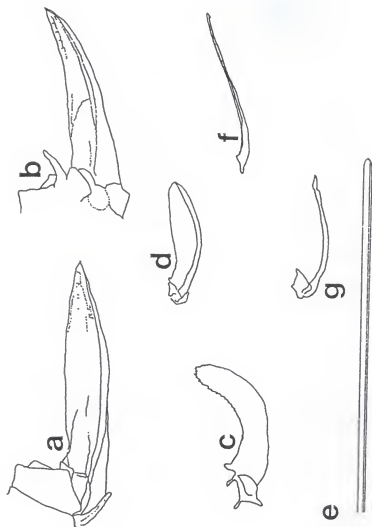


Fig. 3-3.--Ovipositors of female katydids (a-e), cricket (f) and cicada (g). These can vary in size from about 5 to 25 mm and can be brown or green.

These are then multiplied by the number of the particular insect eaten. Ants and other scavenging insects can remove or feed on insect remains that accumulate in FGB roosts. Belwood (this study, Chap. 4) found that members of ten species of ants removed about 50% of the wings deposited by bats. These scavengers did not appear to have a taxonomic preference for the insect pieces they removed (*ibid.*).

The most important step in diet determination using the techniques described here is the identification of the bats from which cullings were collected. In cases where bats day roost and feed in the same places, the bats can usually be caught with an insect net or mist nets as they exit at dusk to feed (see Tuttle 1976). In roosts that are used only for feeding, the bats must be caught as they enter or exit the roosts to feed.

In general, FGB appear to tolerate only one or two capture episodes at a roost before abandoning it permanently. They will tolerate repeated (e.g., semi-weekly or weekly) visits to a day roost to collect cullings, however, providing that they roost in a relatively inaccessible space (e.g., high up in a hollow tree). However, if the bats are clearly visible or are hanging in the open, as in a cave, they will abandon a roost permanently if approached more than a few times--even if only to collect wings. In such cases, cullings should be collected at night, when the bats have left to forage. With

care and practice, it is possible to catch, mark (Handley, in preparation), identify and monitor long term patterns in feeding in any one group of bats over several months (Wilson 1971; LaVal and LaVal 1980^{a,b}) or years (Belwood this study, Chap. 4).

Although the examination of culled insect parts is best suited for diet determination in FGB, the technique can also be applied to aerial insectivores. Poulton (1929) successfully collected moth wings beneath the roosts of Plecotus auritus (Vespertilionidae) in England. Similarly, Belwood and Fullard (1984) collected and identified large numbers of moth wings from Lasiurus cinereus that were dropped as they foraged in an isolated area in Hawaii. This was possible because L. cinereus and their prey were clearly visible as they foraged at bright lights, and this is the only bat found in Hawaii. In this case, large numbers of prey could accurately be identified to species, which is usually not possible in aerial insectivores. Although other, and probably most, aerial insectivore bats will be found to cull insect pieces as they fly (see p. 35) and feed (Coutts, Fenton and Glen 1973; Kunz 1974), recovering these from beneath actively foraging bats is probably not feasible because the bats producing the pieces cannot be accurately identified as they fly in the field.

Conclusion

Regardless of what bats eat or how they forage, diet determination in members of most insect-eating species is difficult. Largely, this is because bats are nocturnal and because they fly, sometimes over very long distances, and thus cannot be followed or observed easily as they feed.

Historically, fecal analysis and stomach content analysis have been the 'standard techniques' used to determine diet in bats. Although large numbers of individuals can be collected from bat roosts or flyways (regularly travelled flight paths) for these purposes, low disturbance thresholds can reduce trapping success rapidly (in as little as three or four days). Moreover, highly efficient mastication, rapid transit time of food through the gut, and biases associated with fecal and stomach content analysis reduce the quality and quantity of data that can be obtained using these techniques. Fecal analysis rarely allows the insects eaten to be identified taxonomically beyond the level of order, and results may be biased toward hard-bodied insects.

Consequently, the results of many bat feeding studies are anecdotal lists that vaguely describe "who ate what when". Characteristically, "when" usually consists either of a very short period of time (e.g., a few hours to a few evenings), or a very long period of time (e.g., several years, when all the material that is opportunistically

collected from bats within a certain area is lumped together). Such studies are not very meaningful as they do not address important ecological questions, specifically those that concern how bat diets change seasonally as a function of the qualitative and quantitative changes in insect availability, and as a function of the changing energy requirements of specific life history phases (e.g., reproduction, hibernation, migration). For aerial insectivore bats, the studies of Kunz (1974) and Anthony and Kunz (1977) stand out as exceptions to this generalization. They are also good examples of how feeding studies should be done, if chiroptologists are to progress from merely cataloguing the prey taken by bats to answering important ecological questions.

An ecologically meaningful approach to bat feeding requires long term studies. It is important to note that such studies are not possible if a large number of individuals are studied using destructive techniques (e.g., collection of stomachs). In some instances, especially when small colonies are concerned, a choice must be made between sacrificing animals and the observation of the same individuals over a longer period of time. The increasing availability of sophisticated monitoring devices such as night vision scopes and ultrasound detectors has opened up a new set of possibilities with respect to the study of bat feeding ecology. In particular, in the future these devices

should be used to study, in greater detail, the foraging habitats and microhabitats of more bat species and to provide much needed information about how they locate and handle prey. Much of this can be done with minimal disturbance to animals in the field.

Laboratory studies that combine free flying bats with natural prey items in large flight cages are useful in bat feeding studies, and have not been used to their fullest potential. While it is naive to think that natural foraging situations can be recreated artificially, a surprising amount of information can be obtained from such studies to supplement information that is gathered in the field. For example, basic information can be obtained about how bats forage (on the wing or from perches) and about what kind of prey they take and how these are handled.

Foliage gleaning and flycatching bats in both the Old and New Worlds are particularly good candidates for long term feeding studies because they occur in small groups, forage from a few 'traditional' feeding perches, have relatively small feeding ranges, and only spend a short period of time on the wing. Marked individuals have been observed for periods lasting almost a year. The studies of Vaughan (1976, 1977) and Vaughan and Vaughan (1986) illustrate beautifully the type of information that can be obtained when gleaners and flycatching bats are observed over a long period of time.

These bats also feed on large insects whose remains are deposited on the ground and can easily be recovered, identified (in many cases to species) and quantified (both numerically and in terms of biomass). Also, the fact that prey species can often be positively identified, and even sexed, which is usually not possible with bats that feed on small insects on the wing, reveals a great deal about where and how these bats forage. The precise nature of prey species eaten can also be used to address questions pertaining to how resources are partitioned by bats in a given community. This is not possible with aerial insectivores.

Fecal analyses alone should not be used to determine diet in foliage gleaning and flycatching bats as most of the taxonomically important pieces of their insect prey are culled and the results of such a study are likely to be biased and incomplete. As such, finding the feeding roosts of these bats is essential to the determination of diet, and their contents cannot be ignored. Based on fecal analysis, and with very small sample sizes, Humphrey, Bonaccorso and Zinn (1983), for example, report that the FGB of BCI comprise a beetle eating 'guild'. The results reported by Belwood (this study, Chap. 4) that span a two year period and describe the remains of almost 25,000 insects eaten by two bat species, support the finding that beetles are

important in the diets of these bats, but dispute the notion of beetles as a primary food source.

Biases are associated with all the techniques that are currently available to determine diet in bats. The use of culled insect fragments is no exception. First, because wings are the most commonly deposited insect remains, and the easiest to identify, flightless insects (e.g., nymphal katydids and roaches, spiders and caterpillars) are likely to be overlooked. Second, ants and other scavengers may remove some of the insect pieces that accumulate in bat roosts. Every attempt should be made to control for this. Third, if the bats under study have more than one feeding roost, a portion of the insects taken may be unavailable.

The techniques used to study feeding ecology in a particular species or community will vary according to the nature of the bats and questions under study. As many methods as possible should be used in order to determine which technique(s) is (are) best for given circumstances. In the case of aerial insectivores, fecal and/or stomach content analyses may be the only methods possible to determine diet. If this is the case, several factors should be considered. Large colonies, for example, will tolerate repeated netting and removal of individuals for their stomachs, or disturbance to individuals for feces collection better than smaller ones [e.g., the Micronycteris colonies

studied on BCI that contain only a dozen or so individuals; Belwood this study (Chap. 4)]. The latter could be totally destroyed after only one or two collecting episodes. In such cases, the biases associated with fecal analysis may be outweighed by the information gained in a long term study. In the case of the foliage gleaners, the study of roost cullings is the best way to determine diet. Also this allows a level of detail to be achieved in results that is not possible in the study of aerial insectivores.

CHAPTER 4
DIET OF FOLIAGE GLEANING BATS, PARTICULARLY
Micronycteris megalotis AND M. hirsuta ON BARRO COLORADO
ISLAND, PANAMA

Introduction

Little is known about prey selection in neotropical phyllostomine bats (Gardner 1977). Between December 1982 and December 1984, various aspects of feeding (Belwood this study, Chap. 3) were studied in the phyllostomine bats of Barro Colorado Island, Lake Gatun, Panama (9°09'N, 79°52'W) (BCI). The species for which data were collected include Micronycteris megalotis, M. schmidtorum, M. hirsuta, M. brachyotis, M. nicefori, Macrophyllum macrophyllum, Tonatia bidens, T. silvicola, Mimon crenulatum, Phyllostomus discolor, P. hastatus, Phylloderma stenops, Trachops cirrhosus, and Chrotopterus auritus.

Materials and Methods

Feces Collection--Wild Bats

Bats were routinely netted in the field, in dense forest, for the collection of feces, which were oven dried for 24 h at 80°C, weighed and counted. Each pellet was teased apart under a dissecting microscope in a dish containing 70% ethanol. Prey items were identified to order

when possible, and were quantified as percent volume, as in Belwood and Fenton (1976) and Whitaker (1988).

Roost cullings--wild bats

Twenty-seven M. megalotis, and 11 M. hirsuta feeding roosts were found. When possible, insect remains were collected from these several times per week. For nearby roosts, weekly visits ranged from one to three depending on the roost's location and the ease with which it could be reached.

Members of ten species of scavenging ants (Atta colombia, Azteca sp., Monachis sp., Odontomachus sp., Pachycondyla villosa, P. sp., Pheidole 2 spp., Wasmannia sp., and an unidentified ponerine), and nymphs of the giant cockroach, Blaberus giganteus, were found living in the substrates of many of the bat roosts that were studied. In order to determine what proportion and taxa of insect remains, if any, were removed by these insects, 40 fresh insect wings, obtained from insects that were collected at ultraviolet lights and killed by freezing, were placed in each of eight active bat roosts from which culled insect fragments were routinely collected. Each wing was marked with a drop of white Liquid Paper® and was left in the roost for three days before being retrieved. Ten wings of 4 'types' were used. These were 'hard' (beetle forewings), 'leathery' (katydid and roach forewings), 'cellophane'

(cicada and dragonfly wings), and 'scaly' (moth wings).

This was repeated 4 times for a total of 1280 wings.

Captive feedings

Thirty-four bats--12 M. hirsuta, 8 T. silvicola, three T. bidens, 4 T. cirrhosus, 3 M. megalotis, and 1 each C. auritus, M. nicefori, M. schmidtorum, and P. stenops were fed in captivity, three times per night (at 1830, 2400, and 0500 h) in small hardware cloth cages (24 by 20 by 15 cm) for one to several nights in order to observe their handling of prey, and to compare the results of fecal analysis with the results from an examination of insect cullings as methods to determine diet. To maintain good health, the bats were allowed to fly freely in a small room for about an hour each night. All the bats captured were released.

Forceps were used to present bats with whole, live insects, or other prey, known to approximate natural diets in the field (Wilson 1971; LaVal and LaVal 1980a; Belwood this study). These included katydids (winged adults and wingless last instar nymphs), beetles, moths, cicadas (winged adults), cockroaches, crickets, dragonflies, and assorted other insects ('catch of the day') when they were available. When available, both 'large' (20-50 mm body length (BL)) and 'small' (<20 mm BL) insects were used as food. T. cirrhosus were also fed live frogs (Physalaemus pustulosus--Leptodactylidae). Each bat was also presented a fruit, sugar and water solution (water mixed with dissolved

unflavored glucose tablets, table sugar and mashed papaya and banana) from an eye dropper. Culled insect parts and feces were collected, separated, and number coded for each bat. These were then examined separately several months later, and the results of each analysis compared.

In order to determine prey biomass for different insect types, live weights were obtained for 634 insects, both with and without their wings and legs (since bats remove wings and legs). These included 189 beetles (Coleoptera), 101 katydids (Orthoptera: Tettigoniidae), 35 cockroaches (Orthoptera: Blattoidea), 132 moths (Lepidoptera: various families), 77 cicadas (Homoptera: Cicadidae), and 20 dragonflies (Odonata: various families). In addition, all items consumed by T. cirrhosus and C. auritus were weighed.

Results and Discussion

Captive feedings

All the bats ate in captivity, except M. schmidtorum, which refused to eat and was released. However, M. nicefori, P. stenops, and C. auritus refused insects that were presented as food. M. nicefori and P. stenops readily accepted the liquid fruit mixture and C. auritus ate only pieces of raw chicken. These results are in agreement with the little already known about the diets of these bats (Gardner 1977). C. auritus is believed to feed on small vertebrates, while M. nicefori and P. stenops feed mainly on

fruit. The remainder of the bats consumed insect prey with gusto, and T. cirrhosus accepted both insects and frogs. In addition, these bats refused the fruit mixture but drank plain water, supporting the idea that they do not regularly feed on fruit.

All the bats kept well in captivity except M. nicefori and M. megalotis. These bats are small (about 6 g) and require almost constant feeding in order to maintain body weights. The larger bats (Tonatia spp., T. cirrhosus, and C. auritus) could be kept for up to a week without adverse effects, providing they were fed regularly, i.e., several times per night and always just prior to dawn. All the bats captured were released.

Feeding behavior of the bats in captivity was stereotyped. Even in a small cages, the bats were alert and hung by one or two feet from the top of their cages. With their feet stationary, they rotated their bodies constantly covering an arc of about 90°. This was accompanied by rapid, almost continuous twitching of the pinnae.

In the large flight cage, bats were allowed to 'feed themselves' by finding their own prey. They usually flew to male katydids that called, or to other large insects like roaches, that scurried about on a leaf litter covered floor. These bats did not pursue moths that flew about a 25 watt red light at the top of the flight cage, nor did they

attempt to feed on any other prey that entered and flew about the flight cage.

All prey were consumed in the same manner. In most cases, the bats used their wings and thumbs to position an insect in their mouths. If the insect was dropped and fell to the bottom of the feeding cage, the bat pounced on it, grabbed it by the thorax in its mouth, and returned to its feeding perch.

The bats waited motionless at their perches, with insect in mouth, between 10 s (in the case of insects with $BL < 20$ mm) and several minutes (insects 40 to 50 mm BL) before they began to feed. The insects were always held by the thorax (their 'locomotion centers'), which was crushed by the bat's teeth. This subdued the insects, as they were never observed to struggle. This is noteworthy because many of these insects consumed, and also those captured by these bats in the field (mainly katydids--see below) are equipped with sharp spines on their legs, which could injure a bat. The insects were consumed anterior to posterior, beginning from the head, and were periodically repositioned with the bats' thumbs, as diagrammed for *N. thebaica* by Fenton, Gaudet and Leonard (1983). Insect wings and legs were culled in sequence, first the fore then the hind wings, then the three sets of legs, respectively. Occasionally, the first pair of legs was eaten. Even wings of the small beetles and flies ($BL < 15$ mm) were culled. When bats ate

prey without wings (last instar nymphs, spiders and caterpillars), only the legs, legs, or head capsules, respectively, dropped to the floor, indicating that wingless insects may go undetected if culled wings alone are used to determine diet. Unfortunately, as stated in Chapter 3, insect legs can be difficult to identify taxonomically. The bats consumed the abdomens of the first few insects they ate, but discarded GI tracts of subsequent ones. In the case of katydids, female ovipositors, which are hard and protrude beyond the abdomen (Fig. 3-3), and eggs, which are also hard and are packed in the abdomen, were discarded. The average time required for T. silvicola and M. hirsuta to consume a moderately sized insect (BL 30 to 40 mm) was $8'32 \pm 5'27$ s ($n = 25$).

Katydid and cicadas were the preferred prey of the bats in captivity. They became very excited when these insects were presented to them. However, katydids with pronounced thoracic spines [e.g., Steirodon careovirgulatum (Phaneropterinae)] were always refused. During the dry season, when the insects available to feed bats were scarce, these katydids were accepted providing their spines were first removed with scissors. Almost all other insects were consumed by the bats although they appeared reluctant to feed on moths. The scales on these insects made many of the bats, particularly T. bidens, sneeze and rub their faces and eyes for several minutes.

Three T. bidens (average empty weight = 31.9 g) and three T. silvicola (average empty weight = 26 g) were weighed immediately before and after feeding. The former consumed an average of $14.1 \pm 5.44 \%$ of its body weight per feeding ($n = 15$ feedings), the latter $16.2 \pm 5.49 \%$ ($n = 12$ feedings). Optimally, if the bats fed three times per night in the field, which is a reasonable assumption, they would consume almost half their weight in insects. These figures are in agreement with others that show that bats in general are voracious feeders, and take about 30 to 50% of their body weights in insects per night (Constantine 1970). Silva Taboada (1979:136) reports average stomach contents of Macrotus waterhousii, another foliage gleaning phyllostomine in Cuba, that represent over 25% of the animals' body weights.

The (60 g) C. auritus ate a total of 30 g of raw chicken on each of four consecutive nights without weight loss. The average number of frogs (mean weight 1.9 ± 0.3 g, $n = 20$) consumed by four T. cirrhosus in one night was 10.2 ± 2.1 , each of which was consumed in an average of $7 \text{ min } 36 \text{ s} + 1 \text{ min } 24 \text{ s}$). The frogs were grabbed by the head or upper abdomen and were consumed whole, including all bones and skin, from anterior to posterior. Periodically during feeding, the bats rubbed the fleshy tubercles on their lips (Nowak and Paradiso 1983) back and forth in the frogs' viscerae. The GI tracts belonging to all but three frogs

were eaten. Those that were discarded were infested with live nematodes, indicating that in addition to sensing the toxins present in the skins of some frogs (Tuttle, personal communication), the tubercles may function to help bats identify prey that are parasitized.

Fecal Analysis of Captive Bats

The bats produced fecal pellets about 45 minutes after consuming their first prey items (Table 4-1). Seven T. silvicola that ate 41 insects produced 195 pellets for an average of 7.4 ± 5.1 pellets per insect consumed. Similarly, 12 M. hirsuta that ate 50 insects produced 7.9 ± 4.6 pellets per insect. The 14 insects fed to three T. bidens produced 112 pellets (9.1 ± 3.8 pellets per insect), and three M. megalotis ate 34 insects producing 6.2 ± 1.6 pellets per insect. In contrast, the carnivorous bats produced the fewest number of pellets, presumably because their prey lack the hard, undigestible exoskeletons of insects. Four frog-fed T. cirrhosus produced 38 pellets after eating 19 frogs (3.0 ± 2.7 pellets per frog), and on three occasions C. auritus produced only three after consuming more than 20 g of chicken.

The finding that insect-eating bats produced a large number of fecal pellets per insect consumed, and an even larger number (average: 29.9 ± 9.6) per feeding bout, is important. Students of bat feeding ecology often have

Table 4-1.--Results of fecal analysis of captive hand fed foliage gleaning bats of Barro Colorado Island, Panama. Orth = Orthoptera, Col = Coleoptera, Lep = Lepidoptera, Hym = Hymenoptera (ants), Trach = pieces of acoustic tracheae of katydids and crickets, Ant = antennal segments, FW = pieces of front wing, HW = pieces of hind wing, tr = trace amounts. Katy = katydids, Beet = beetles, Cic = cicadas, Drag = dragonflies, Antl = antlions, Gras = grasshoppers, PLHP = planthoppers, Roch = roaches, Cric = crickets.

BAT SPECIES (% I.D. NUMBER)	# PELLETS	INSECTS EATEN		INSECTS EATEN										PELLETS W/ IDENTIFIABLE PARTS	
		INSECT	INSECT	Katy	Beet	Roch	Cic	Drag	Antl	Gras	Fly	PLHP	Roch	Cric	Number
<i>T. silvicola</i> (1)	33	12	2.8	3	4	0	1	1	1	1	1	0	0	0	8/33
<i>T. silvicola</i> (18)	33	6	5.2	2	0	0	0	0	0	0	0	0	0	0	28/33
<i>T. silvicola</i> (19)	31	6	5.2	4	0	0	0	1	0	0	0	0	0	0	32/31
<i>T. silvicola</i> (20)	26	4	6.5	2	0	0	0	0	0	0	0	0	0	0	24/26
<i>T. silvicola</i> (22)	16	9	1.8	4	0	0	1	1	1	0	0	0	1	1	2/16
<i>T. silvicola</i> (28)	36	4	9.0	1	0	0	1	0	1	0	0	0	0	0	6/36
<i>T. silvicola</i> (30)	16	2	8.0	0	1	0	1	0	0	0	0	0	0	0	10/16
<i>M. hirsuta</i> (2)	14	1	14.0	0	0	1	0	0	0	0	0	0	0	0	8/14
<i>M. hirsuta</i> (5)	26	6	4.3	4	0	0	1	0	0	0	0	0	0	0	12/43
<i>M. hirsuta</i> (6)	26	6	4.3	4	0	0	1	0	0	0	0	0	0	0	21/26
<i>M. hirsuta</i> (7)	14	1	14.0	1	0	0	0	0	0	0	0	0	0	0	9/14
<i>M. hirsuta</i> (9)	2	3	7.7	3	0	0	0	0	0	0	0	0	0	0	9/23
<i>M. hirsuta</i> (10)	5	3	5.0	1	0	0	1	1	0	0	0	0	0	0	1/15
<i>M. hirsuta</i> (12)	17	15	1.2	4	0	0	1	2	2	1	1	1	1	1	9/17
<i>M. hirsuta</i> (16)	10	1	10.0	1	0	0	0	0	0	0	0	0	0	0	1/10
<i>M. hirsuta</i> (20)	23	1	4.0	0	0	0	0	0	0	0	0	0	0	0	0/4
<i>M. hirsuta</i> (27)	23	1	4.0	0	0	0	0	0	0	0	0	0	0	0	7/23
<i>M. hirsuta</i> (31)	45	3	12.0	2	0	0	1	0	0	0	0	0	0	0	8/45
<i>M. hirsuta</i> (32)	29	3	9.7	0	1	1	0	1	0	0	0	0	0	0	17/29
<i>T. bidens</i> (3)	38	4	9.5	3	0	1	0	0	0	0	0	0	0	0	8/38
<i>T. bidens</i> (25)	38	3	12.7	2	0	1	0	0	0	0	0	0	0	0	38/38
<i>T. bidens</i> (26)	3	7	5.1	3	0	1	0	0	0	0	0	0	0	0	12/36
<i>M. nivalis</i> (14)	14	21	5.4	5	4	1	1	2	1	0	2	1	2	2	45/114
<i>M. nivalis</i> (15)	40	1	5.8	2	2	0	1	3	0	0	2	0	0	1	20/40
<i>M. nivalis</i> (36)	5	1	5.0	0	0	0	0	0	0	0	0	0	0	0	0/5
<i>T. cirrhosus</i> (4)	7	3 frogs	2.3	0	0	0	0	0	0	0	0	0	0	0	0/7
<i>T. cirrhosus</i> (31)	7	2 frogs	3.5	0	0	0	0	0	0	0	0	0	0	0	2/7
<i>T. cirrhosus</i> (34)	20	11 frogs	1.8	0	0	0	0	0	0	0	0	0	0	0	0/20
<i>T. cirrhosus</i> (35)	4	3 frogs	1.3	0	0	0	0	0	0	0	0	0	0	0	0/4

Table 4-1.--continued.

BAT SPECIES (& I.D. NUMBER)	FECS WITH BEETLE PARTS					FECS WITH KATYDID PARTS					FECS W/ MOTHS					PERCENT VOLUME IN FECS				
	FW	Tarsi	Ant	Leg	HW	Eggs	Leg	Wing	Mouth	Trach.	Ant	Other	Scales	Orth	col	Lep	Hym	Hair	Skin+	Soil ?
<i>T. silvicola</i> (1)	1	2	1	1	1	0	0	0	1	0	0	1	0	tr	1.0	0	0	0	0	99.0
<i>T. silvicola</i> (18)	0	0	0	0	0	0	0	0	1	0	2	6	10	6	tr	0	25.0	0	0	96.2
<i>T. silvicola</i> (20)	0	0	0	0	0	0	0	0	0	0	1	0	22	tr	0	66.6	0	0	3.2	96.8
<i>T. silvicola</i> (22)	0	0	0	0	0	0	0	0	0	0	1	0	0	tr	0	0	0	0	0	100.0
<i>T. silvicola</i> (28)	0	0	0	0	0	1	0	0	0	2	0	3	3	tr	0	0.6	0	0	0	99.4
<i>T. silvicola</i> (30)	1	0	0	1	0	0	0	0	0	2	5	1	0	tr	tr	0.2	0	0	0	99.8
<i>M. hirsuta</i> (2)	0	0	0	0	0	0	0	0	0	0	1	0	7	0.1	0	21.6	0	0	0	78.3
<i>M. hirsuta</i> (5)	0	0	0	0	0	0	0	0	0	2	10	0	22	tr	0	0	0	0	0	100.0
<i>M. hirsuta</i> (6)	0	0	0	0	0	0	0	0	1	0	0	0	0	tr	0	16.7	0	0	0	100.0
<i>M. hirsuta</i> (7)	0	0	0	0	0	0	0	0	0	0	0	0	0	tr	0	0	0	0	0	100.0
<i>M. hirsuta</i> (9)	0	0	0	0	0	0	0	0	0	7	1	0	0	tr	0	0	0	0	0	100.0
<i>M. hirsuta</i> (10)	0	0	0	0	0	0	0	0	0	0	0	0	0	tr	0	0	0.1	0	0	99.9
<i>M. hirsuta</i> (12)	0	0	0	0	0	0	0	0	0	1	0	0	7	tr	0	13.3	0	0	0	86.7
<i>M. hirsuta</i> (16)	0	0	0	0	0	0	0	0	0	0	0	0	0	tr	0	0	0	0	0	100.0
<i>M. hirsuta</i> (27)	0	0	0	0	0	0	0	0	0	0	0	0	0	tr	0	0	0	0	0	100.0
<i>M. hirsuta</i> (29)	0	0	0	0	0	0	0	0	0	0	0	0	0	tr	0	0	0	0	0	100.0
<i>M. hirsuta</i> (31)	0	0	0	0	0	0	0	0	0	0	0	0	4	tr	0	0.1	0	0	0	99.9
<i>M. hirsuta</i> (32)	0	0	1	0	0	0	0	0	0	0	2	2	4	tr	0	0.1	0	0	0	99.9
<i>T. bidens</i> (3)	0	0	0	0	0	0	0	0	0	0	0	0	5	0	tr	0.1	0	0	0	99.9
<i>T. bidens</i> (25)	0	0	0	0	0	0	0	0	0	0	1	3	2	2.6	0	25.0	0	0	0	72.4
<i>T. bidens</i> (26)	0	0	0	0	0	0	0	0	0	0	1	0	38	tr	0	33.0	0	0	0	67.0
<i>T. bidens</i> (36)	0	0	0	0	0	1	1	0	0	0	0	7	2	tr	0	14.3	0	0	0	85.7
<i>M. megalotis</i> (14)	0	0	5	0	0	0	0	1	1	5	8	0	24	tr	tr	4.9	0	0	0	95.2
<i>M. megalotis</i> (15)	0	0	1	0	0	0	0	0	0	0	1	0	8	tr	tr	1.1	8.3	0	0	90.6
<i>M. megalotis</i> (36)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	100.0
<i>T. cirrhosus</i> (4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100.0
<i>T. cirrhosus</i> (33)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22.5 77.5
<i>T. cirrhosus</i> (34)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12.9 44.3 42.8
<i>T. cirrhosus</i> (35)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5.0 94.0 1.0
<i>T. cirrhosus</i> (35)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6.0 94.0 0

Table 4-1.--continued.

BAT SPECIES (# I.D. NUMBER)	PARTS FROM UNKNOWN ORDERS						
	Tarsi	Gut	Cerci	Eyes	Mouth	HW	Legs Ant Head
					parts		
T. silvicola (1)	1	0	0	0	2	0	0
T. silvicola (18)	0	0	0	0	1	0	0
T. silvicola (19)	0	0	0	0	1	0	0
T. silvicola (20)	0	0	0	0	2	0	0
T. silvicola (22)	0	0	0	0	0	0	0
T. silvicola (28)	2	1	0	0	5	1	0
T. silvicola (30)	0	0	1	2	1	0	0
M. hirsuta (2)	0	0	0	0	0	0	1
M. hirsuta (5)	0	0	0	0	0	0	0
M. hirsuta (6)	0	0	0	0	0	0	0
M. hirsuta (7)	0	0	0	0	0	0	0
M. hirsuta (8)	0	0	0	0	0	0	0
M. hirsuta (9)	0	0	0	0	0	0	0
M. hirsuta (10)	0	0	0	0	0	0	0
M. hirsuta (12)	0	0	0	0	0	0	0
M. hirsuta (16)	1	0	0	0	1	0	0
M. hirsuta (27)	0	0	0	0	0	0	0
M. hirsuta (29)	0	1	0	0	2	0	0
M. hirsuta (31)	1	1	1	0	2	0	0
M. hirsuta (32)	1	1	1	0	1	0	0
T. bidena (3)	0	0	0	0	0	0	0
T. bidena (25)	0	0	0	0	0	0	0
T. bidena (26)	1	0	0	1	0	0	0
M. megaliotis (14)	8	0	0	6	4	0	0
M. megaliotis (15)	0	1	0	4	5	0	0
M. megaliotis (16)	0	0	0	0	0	0	0
T. cirrhosus (4)	0	0	0	0	0	0	0
T. cirrhosus (33)	0	0	0	0	0	0	0
T. cirrhosus (34)	0	0	0	0	0	0	0
T. cirrhosus (35)	0	0	0	0	0	0	0

access only to small fecal samples. For example, the average number of fecal pellets examined in the study of FGB feeding habits by Humphrey, Bonaccorso and Zinn (1983) was about 2.5 per animal, and 8 to 48 per species. This means that the conclusions reached in this paper--that the FGB of BCI represent a beetle-eating guild--are based on the remains of less than one insect consumed per bat. In view of the results presented here, that a large number of pellets are produced per prey item consumed and per meal (using prey that realistically represented prey eaten in the field), care should be taken when interpreting the results of fecal studies using very small samples.

The captive FGB in this study culled most of the taxonomically important body parts from insects prior to eating them. As a result, only half (53.0%) of the 784 fecal pellets collected from the bats fed in captivity contained insect parts, other than 'exoskeleton', that could be recognized (e.g., 'tarsal claw', 'portion of eye') (Table 4-1). Only 31.1% contained pieces that could be ascribed to an insect family or order (e.g., 'katydid tarsus', 'beetle antenna'). Identification below the family or ordinal level in these cases was usually impossible. It is noteworthy that many of the katydids fed to the bats were green when alive, but were yellow after passage through the digestive tract.

Moth scales [present in 162/784 pellets (20.1%)] were the most common and easily recognizable insect parts, followed by "small pieces of filiform Orthoptera (roach or katydid) antenna", which were found in 59/784 pellets (7.5%). The acoustic tracheae of katydids and crickets, internal structures that aid in audition and are peculiar to these insects (Morris, Klimas and Nickle, in press: Fig. 11e), were the next most commonly found pieces (in 29/784 pellets or 3.7% of the pellets). The remainder of the pieces found are listed in Table 4-1, but identification of these below the ordinal level was not possible.

Using fecal analysis, it was impossible to quantify the number of insects that were fed to the captive bats. Although 138 insects were eaten, the items listed in Table 4-1, when added together to 'reconstruct' whole insects, indicate only that one katydid each was taken by 22 of the bats and that one beetle each was eaten by four bats. The one exception is M. megalotis (bat number 14), where five scarabaeid antennae were found, indicating that at least three beetles were consumed. The results also show that moths were taken by 13 bats and that the four Trachops consumed vertebrates. The small bones of P. pustulosus were fragmented in the feces, and could not be identified specifically or counted. No trace of the cicadas, ant lions, dragonflies, walking sticks, leafhoppers, flies, or grasshoppers that were fed to the bats were found because

the wings of these insects were culled. These results indicate that many of the insects eaten by FGB go undetected when the diet is analyzed using fecal analysis. The same would probably hold true for stomach content analyses. Furthermore, when insects could be identified, the number eaten could not be determined.

All the insects consumed, with the exception of the wingless, immature katydids ($n = 11$), were accounted for when insect cullings (wings) were examined. This includes insects whose wings were only 5 to 10 mm long.

Several intact ant heads or ants (< 1 mm BL) were found in the feces of the captive M. hirsuta, T. silvicola, and T. cirrhosus. These probably represent prey of some of the insects or frogs that were eaten by these bats.

In general, fecal analysis does not appear to be a good method to determine diet in FGB. Unlike the findings of Kunz and Whitaker (1983), this does not appear to be a function of digestion due to passage through the digestive tract, but occurs because taxonomically important pieces of the insects consumed are culled. The insect pieces that do pass through the GI tract are difficult to identify, and moths are likely to be over-represented.

Fecal Analysis of Wild Caught Bats

In spite of the above-mentioned limitations and biases, 1000 fecal pellets were examined from 156 wild caught FGB bats on BCI (Table 4-2). These represented nine species.

Plant matter (undigested plant matter and seeds) dominated in the diets of P. hastatus and M. nicefori, which agrees with the results of the captive feedings study (for M. nicefori) and published information on diet in these bats (Gardner 1977, Bonaccorso 1979). Each of these bats also produced a relatively small number of fecal pellets per individual, which is consistent with a diet that includes fleshy fruit but not insects.

Small beetles (5 to 10 mm BL based on recognizable body parts; 76% of diet) and moths (size unknown; 100%) dominated in the diets of the few M. crenulatum and M. macrophyllum that were captured. In his summary of phyllostomid feeding habits, Gardner (1977) lists only 'insects' as the prey of both species, and principally what appeared to be aquatic species as the prey of the latter. Results of the present study offer no additional information as to the specific nature of the insects taken, what microhabitats they are found in, or how they were captured. Whether or not these two bats are gleaners in the true sense of the word remains to be seen. The small size of the beetles taken by M. crenulatum indicates that they probably are not.

Table. 4-2.--Prey of wild caught phyllostomine bats from Barro Colorado Island, Panama, based on fecal analysis. Values are mean percent in all fecal pellets.

BAT SPECIES [FOREARM (mm)]	# OF BATS/FECES	ORTHOP- TERA	COLEOP- TERA	LEPIDOP- TERA	OTHER INSECT	? INSECT	BONE	SOIL	FRUIT	MUCOUS SEED
<u>M. macrophyllum</u> (34-37)	5/59	-	-	100	-	-	-	-	-	-
<u>M. hirsuta</u> (42-45)	18/130	52.7	22.2	-	-	18.6	-	6.5	-	-
<u>M. megalotis</u> (30-34)	18/90	66.0	18.0	0.6	5.0	-	-	-	4.0	6.4
<u>M. nicefori</u> (37-40)	4/4	-	-	-	-	0.5	-	-	99.5	-
<u>M. crenulatum</u> (48-52)	12/103	14.8	76.6	1.9	-	4.3	-	2.4	-	-
<u>P. hastatus</u> (81-85)	3/9	-	-	-	-	20.0	-	-	80.0	-
<u>T. bidens</u> (55-60)	35/194	31.7	7.7	3.6	-	54.5	-	-	-	2.5
<u>T. silvicola</u> (51-53)	47/367	83.8	1.8	0.4	1.3	10.6	-	1.1	1.0	-
<u>T. cirrhosus</u> (57-61)	14/44	39.2	27.7	-	3.7	5.8	8.1	13.4	2.1	-

When insects could be identified, Orthoptera appeared to dominate in the diets of most of the remaining bats (*M. hirsuta*, *M. megalotis*, *T. silvicola*, *T. bidens*, and *T. cirrhosus*) as indicated by the presence of body parts--particularly long filamentous antennae and acoustic tracheae. These could not be positively identified, but appeared to be from large cockroaches, katydids, or crickets based on color. Soil and small bone fragments were found in the feces of *T. cirrhosus*, indicating that they had fed partly on ground dwelling vertebrates. More than half of the insect prey of *T. bidens* could not be identified to order.

Beetles were also important in the diets of three of these species (*M. hirsuta*, *M. megalotis*, and *T. cirrhosus*) and comprised about 20 to 25% of the volume of the feces.

With the exception of *M. macrophyllum*, none of the bats appeared to prey heavily on Lepidoptera; therefore, Black's (1972, 1974) technique to determine the relative importance of these insects in the diet was not used. This agrees with the general reluctance of the captive fed bats studied here to feed on moths. Moths are abundant on BCI throughout the year, and are likely to be one of the most consistent insect resources there (Belwood, in preparation). Worldwide, they are also preyed on heavily by a variety of bat species. Other New World FGB feed on these insects in large numbers (e.g., *Macrotus waterhousii* in the West Indies; Belwood,

unpublished data). Why these insects are apparently ignored by the majority of FGB on BCI is not known.

Roost Cullings

Marked Insect Wings

Approximately one half (605 or 47.3%) of the 1280 marked insect wings deposited in hollow trees were removed by the ants and other insects that are found in active bat roosts (Fig. 4-1). However, there was no significant preference for one type of insect wing over another--all were removed in approximately equal proportions.

Insect Prey of *M. megalotis*

Twenty seven *M. megalotis* roosts were found. The majority (14/27) were hollow cavities in live, standing trees. Most openings to these originated on the ground, and all were 0.5 to 1.5 m high and 0.3 to 0.5 m wide. Seven roosts were large hollow cavities in dead trees (1 m diameter) that were lying on the ground. Roost openings had also been at the (former) bases of these trees. Two additional roosts were under large (dbh 70 cm) dead trees that had fallen to the ground, but were partly supported by tree stumps forming a space with a height of about 0.5 m between the tree and ground. The four remaining roosts, respectively, were in a large, partly hollow tree stump (2 m diameter, 1 m high), in a small abandoned concrete shed

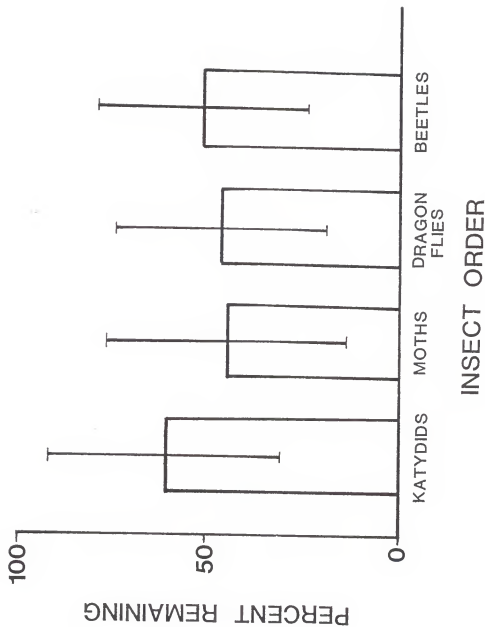


Fig. 4-1.--Percentage of marked insect wings remaining in bat roosts after 3-day exposure to ants and other scavenging insects. Four types of wings are represented: 'leathery' (katydidids), 'scaly' (moths), 'cellophane' (dragonflies and cicadas), and 'hard' (beetles).

missing half it's roof, under the palm thatched roof of a small wall-less "bohio", and under the tin eaves of a small abandoned building.

All but two of the roosts were in dense forest and away from water. The exceptions were the "bohio" roost, which was in a cleared area, on the forest edge, approximately 25 m from the edge of Lake Gatun, and the concrete shed, which was at the edge of a clearing, 3 m from dense forest.

Bats in all the roosts were visible close to openings and could be seen with little trouble. They hung together in small tight clusters of 4 to 12 individuals. In the forest, bats left their roosts to feed approximately 15 minutes before it became too dark for an observer to distinguish forms in the forest without the aid of a flashlight. The bats in the concrete shed, at the forest edge, were observed leaving on their nightly foraging bouts at the same time as the forest bats on 14 evenings. Without exception, they flew directly into the forest. None were observed to fly in or toward the clearing. On bright moonlit nights, these bats remained in their roosts until the moon set.

Eleven of the roosts were inconveniently located and were visited only once. The remainder were visited at least once per week for the collection of prey remains that accumulated in large piles on the ground.

The remains of 12,055 insects were found in the M. megalotis roosts. A wide variety of insects was eaten.

In terms of number, beetles (Coleoptera; 40.9%) dominated in the diet (Table 4-3). The majority of these (27.3%) were small scarabs with body lengths (BL) of 10 to 15 mm. Smaller percentages of click beetles (Elateridae; 6.4%), long horn beetles (Cerambycidae; 1.6%) and weevils (Curculionidae; 1.3%) were taken. These also ranged in size from 10 to 15 mm.

Orthoptera, mainly roaches (Blattoidea; 15 - 20 mm BL; 26.0%) and dragonflies (Odonata; 35 - 45 mm BL; 14.3%) were also important food items. Much smaller amounts of moths (Lepidoptera; 35 - 40 mm BL; 4.0%) and cicadas (Homoptera: Cicadidae; 35 - 40 mm BL; 5.2%) and traces of several other insect groups completed the diet.

In terms of biomass, Orthoptera (40.9%) and Coleoptera (32.3%) were still the most important dietary items (Table 4-3). Among the Orthoptera, crickets (Gryllidae; 20 to 25 mm BL; 17.6%) and cockroaches (16.8%) were represented more or less equally. The small scarabs (23.5%) were the most important beetles eaten with respect to weight.

The majority of the insects eaten were commonly seen on vegetation or on leaf litter on the forest floor. Evidence suggests that BCI's FGB cannot use echolocation to find their prey, but use prey produced sounds instead (Belwood this study, Chaps. 5 and 6). Whether the insects consumed

Table 4-3.--Insect prey consumed by the foliage gleaning bat Micronycteris megalotis over two years on Barro Colorado Island, Panama; as indicated by insect remains collected in 27 bat feeding roosts.

INSECT ORDER	PERCENT BY NUMBER	PERCENT BY WEIGHT
COLEOPTERA		
Scarabaeidae	27.3	23.5
Elateridae	6.4	6.4
Cerambycidae	1.6	-
Curculionidae	1.3	-
Other	4.5	2.4
ORTHOPTERA		
Blattoidea	26.0	16.8
Gryllidae	3.5	17.6
Tettigoniidae	1.4	5.0
Other	0.4	1.5
ODONATA	14.3	11.8
LEPIDOPTERA	4.0	3.6
HOMOPTERA		
Cicadidae	2.3	5.6
Other	2.7	4.2
HYMENOPTERA	2.4	0.9
DIPTERA	1.4	0.5
OTHER	0.5	0.2
<hr/>		
Total	100.00	100.00

by M. megalotis were captured from a substrate or in the air as they flew, or both, is not known.

Two types of insects that commonly occurred on the undersurfaces of leaves were also taken as prey. These were dragonflies and damselflies that hung seemingly motionless and noiselessly from leaves and twigs, and cicadas that were emerging as adults from the last larval instar. How these were located by the bats is not known.

In field experiments, M. megalotis responded to the sexual calling songs of male katydids (Belwood this study, Chap. 6). In spite of this, very few katydids were seen in the prey remains. These constituted only 1.4% and 5.0% of the prey taken, by number and biomass, respectively. The majority of these were small (20 to 25 mm BL) slender green phaneropterines that were not encountered often in the forest.

Insect Prey of M. hirsuta

M. hirsuta used roosting sites similar to those of M. megalotis. Eleven of these were found and all consisted of hollow cavities in live, dead or dying trees in the dense forest. The only visible roost openings were either at ground level, or between 1.5 and 2.0 m off the ground. The presence of additional roost exits higher up on the trees and not visible to an observer is possible but was not documented.

The bats could not be seen inside their roosts, but were captured on several occasions in the two year study period as they exited the main roost opening. The exact number of individuals inhabiting each colony is not known, but appeared to be fewer than ten individuals. The first exit flights from two roosts were monitored on five evenings each, and occurred 15 to 30 minutes after it became too dark for an observer to see in the forest without the aid of a flashlight. This was slightly later than the departures of M. megalotis from their roosts.

M. hirsuta also consumed a variety of insects. By number (Table 4-4), Orthoptera (57.9 %), mainly katydids (Tettigoniidae; 35 - 45 mm BL; 41.1%), roaches (Blattidae; 20 - 35 mm BL; 10.1%), and crickets (Gryllidae; 20 to 30 mm BL; 5.7%) were the most important food items followed by Coleoptera (15 - 25 mm BL; 35.5%), of which a large proportion were scarabs (15 to 20 mm BL) and long horn beetles (20 to 25 mm BL). Much smaller numbers of cicadas (2.9%), dragonflies (1.4%) and moths (1.2%) were eaten.

Orthoptera were even more important in the diet in terms of biomass (Table 4-4) representing about three quarters (74.5%) of the insects eaten. Katydids constituted 61.6%, roaches 8.4%, and crickets 3.8% of biomass.

Scarabs (8.0%) were the most important beetle prey by weight, followed by weevils (3.6%), longhorn beetles (2.5%)

Table 4.4.--Insect prey consumed by the foliage gleaning bat Micronycteris hirsuta over two years on Barro Colorado Island, Panama, as indicated by insect remains collected in 11 bat feeding roosts.

INSECT ORDER	PERCENT BY NUMBER	PERCENT BY WEIGHT
ORTHOPTERA		
Tettigoniidae	41.1	61.5
Blattoidea	0.1	8.4
Gryllidae	5.7	3.8
Other	1.0	0.8
COLEOPTERA		
Scarabaeidae	13.6	8.0
Cerambycidae	10.1	2.5
Elateridae	4.9	1.6
Curculionidae	4.3	3.6
Other	2.6	1.8
HOMOPTERA		
Cicadidae	2.9	6.5
Other	0.4	0.1
ODONATA	1.4	0.8
LEPIDOPTERA	1.2	0.3
OTHER	0.9	0.2

Total	100.00	100.00

and click beetles (1.6%). Cicadas comprised 6.5% of the diets by weight and moths only 0.8%.

Neither M. megalotis nor M. hirsuta were observed as they foraged in the field. Therefore, exactly what cues they use to locate their prey, how and where they feed (on the ground or in the air) are not known. Their choices of prey, however, indicate that at least some foliage gleaning, perhaps in combination with fly-catching, occurs. These bats appear to be fairly specific in their choices of prey, as relatively few taxa are represented.

A detailed description of the prey consumed by M. megalotis and M. hirsuta, including a specific taxonomic breakdown of prey chosen, seasonal differences in diet, prey choice with respect to prey availability, and the factors that are believed to govern prey choice is beyond the scope of this paper and will be presented elsewhere.

Suffice it to say here, that although these bats occur in the same habitats, are caught together in the same mist nets in the field, roost in similar structures, forage at approximately the same times and appear to prey on similar types of insects, their prey differ substantially in taxonomic composition. Where overlap occurs (with roaches, scarab beetles and cicadas), M. megalotis, the smaller bat, feeds on smaller individuals, while the larger M. hirsuta feed on larger individuals.

Katydid prey of M. Hirsuta

Approximately 70 species of katydids occur on Barro Colorado Island (Belwood, unpublished data). Of these, only six species made up the bulk of the katydids eaten (89.5% by number; 92.8% by weight; n = remains of 4498 katydids collected) by M. hirsuta: C. wheeleri (22.9%; 23.1%), Docidocercus gigliotosi (19.1%; 16.4%), Xestoptera cornea (17.1%; 25.8%), unknown pseudophylline "a" (13.4%; 11.5%), unknown pseudophylline "b" (9.8%; 4.4%), and Idiarthron major (7.2%; 11.6%) (Table 4-5). Why members of these six species and not others were taken as prey is not known.

The little that is known about these insects is summarized by Belwood (this study; Chap. 7). All belong to the subfamily Pseudophyllinae. For the most part, they are long, slender, cigar shaped insects that are brownish in color and are usually found at night close to the ground in the lower forest canopy on woody or shrubby substrates. Of the species eaten in large numbers, X. cornea is an exception to this as it is green, somewhat oval in shape, and it occurs in the upper forest canopy as well as closer to the ground. Behaviorally and acoustically, pseudophyllines contrast strongly in appearance and behavior with the more common phaneropterines (Belwood, in preparation), which are the 'typical' leaf-like katydids that are green and usually occur in leafy foliage.

Table 4-5.--Katydid prey of the foliage gleaning bat Micronycteris hirsuta over a two year period on Barro Colorado Island, Panama.

SPECIES	PERCENT BY NUMBER	PERCENT BY WEIGHT
<u>Cocconotus wheeleri</u>	22.9	23.1
<u>Docidocercus gigliotosi</u>	19.1	16.4
<u>Xestoptera cornea</u>	17.1	25.8
unknown pseud. "a"	13.4	11.5
unknown pseud. "b"	9.8	4.4
<u>Idiarthron major</u>	7.2	11.6
Misc. others	10.5	11.6

Total	100.00	100.00

Table 4-6 summarizes some important features about the katydid species eaten by M. hirsuta. In terms of body length, all ranged in size from about 25 to 42 mm, and all weighed between 1 and 3 g. Three of the species were "abundant" (i.e., at least one individual was encountered almost nightly when the insects were in season--D. gigliotosi) or "common" (i.e., individuals were encountered at least once per week when in season--C. wheeleri, X. cornea) in the forest understory on BCI. All were active early in the evening, within a few hours after sunset, which is also the period of greatest bat foraging activity. Conspicuously absent from the diet of M. hirsuta in large numbers was Copiphora brevirostris, another very common katydid in BCI's forest. Members of this species are slightly larger (TL: 60 to 65 mm) than the other insects eaten and they are active later in the evening. This may be responsible for their exclusion in the diet. They were consumed with gusto, however, by captive bats in feeding experiments indicating that they are highly palatable.

FGB on BCI respond to the sexual advertisement calls of male katydids (Belwood this study, Chap. 6). On BCI, this appears to have selected for short, high pitched, sporadically produced calls (Belwood this study, Chap. 7) that are difficult for bats to localize (Belwood this study, Chap. 6). The calling songs of all the katydids taken as

Table 4-6.--Body lengths and weights, and characteristics of the airborne calls of the katydid of Barro Colorado Island, Panama, that are preyed on by the foliage gleaning bat Micronycteris hirsuta. See katydid species accounts for more precise numerical data in each category.

SPECIES	BODY LENGTH		BODY WEIGHT		AIRBORNE CALL CHARACTERISTICS			
	♀ (mm)	♂ (mm)	♀ (mm)	♂ (mm)	Length (s)	Carrier (kHz)	# per 5 Min.	Duty cycle
<u>Cocconotus wheeleri</u>	38.7	37.1	2.3	1.7	0.4	26.0	6.5	0.9
<u>Docidocercus gigliotosi</u>	37.9	36.4	1.8	1.6	0.1	22.4	21.6	0.4
<u>Xestoptera cornea</u>	38.4	34.5	3.6	2.4	0.5	27.5	4.4	1.5
Unknown "a"	37.9	40.0	1.8	1.6	0.5	17.4	5.1	N/A
Unknown "b"	27.3	25.4	0.9	0.9	2.7	17.4	18.8	2.2
<u>Idiarthron major</u>	42.5	42.7	3.6	2.7	0.1	23-27	2.1	0.07

prey fit this general description. They are short in length (average lengths = 0.1 to 2.7 s), and infrequently produced (2.1 to 21.6 per 5 min period). Peak frequencies of the calls are all in the high audio to low ultrasonic range (about 17.4 to 27.5 kHz). In addition, the duty cycles (proportion of time spent singing) of members of all six species are extremely low (0.07 to 2.2%). Although M. hirsuta respond to the calling songs of katydids on BCI, whether these signals are used as the principal cues to locate prey is not known. The short and sporadic nature of the calls would indicate that they are not.

The remains of about 2000 female katydids were found in the M. hirsuta feeding roosts. This was indicated by the presence of a large number of ovipositors and ovipositor pieces in the roost remains. In many cases, damage to the cullings by scavenging insects did not permit the wings of male katydids deposited by bats to be distinguished from those of females, so the proportion of each sex contributing to the diet could not be determined. However, in the case of X. cornea 776 of the 1745 insects eaten could be sexed. Of these, just slightly over half (50.7%) of the insects taken were female.

Until more is known about the biology of BCI's pseudophylline katydids in the field--particularly with respect to the events leading to pair formation, the factors responsible for an apparent equal share of sexes in the diet

cannot be addressed. The large number of females, however, indicates that cues other than male calling song are used to locate prey. This is adaptive, given the short sporadic nature of katydid calls on BCI.

In many katydid mating systems, males call and females respond to them by flying or walking in the direction of the perceived sound signal. Whether this also occurs in species where tremulation is an important signalling cue is not known. In theory, females involved in this behavior could generate sounds that indicate their presence to bats, and this may explain the large number of females taken. Female katydids on BCI are 20 to 40% heavier than their male counterparts (Belwood this study, Chap. 7). Therefore, a foraging strategy in which a large number of this sex is taken as prey would be adaptive.

After mating takes place, females must locate and move to suitable oviposition sites. Observations in the laboratory (Belwood this study, Chap. 7) suggest that females of all the species eaten, with the exception of X. cornea, oviposit in decaying wood, which is often found on the forest floor. In the field, X. cornea females have been collected with soil on their ovipositors, indicating that they oviposit in the soil under leaf litter (ibid.). At most times of the year, the ground on BCI is covered with a layer of leaf litter several inches thick. This produces sound as insects walk through it (Belwood, personal

observation). Because M. hirsuta forage close to the ground, this may bring them into contact with a large number of female katydids.

Conclusions

Much remains to be learned about the feeding habits of New World FGB. The bats appear to be selective at least as to size and taxonomic affinity of prey. Questions concerning the cues used by these bats to locate prey and distinguish between different insect species are of particular interest. Further studies will focus on this as well as on the various aspects of katydid biology that render these insects susceptible to predation by bats.

CHAPTER 5
FORAGING BEHAVIOR, PREY SELECTION, AND ECHOLOCATION
IN THE PHYLLOSTOMINE BATS (PHYLLOSTOMIDAE) OF
BARRO COLORADO ISLAND, PANAMA

Introduction

Most bats use echolocation (biosonar) rather than vision to avoid obstacles, navigate, and locate prey in the dark (Griffin 1958). A thorough knowledge of food habits and feeding behavior is necessary before the adaptive significance of different echolocation types (Simmons, Fenton and O'Farrell 1979) can be appreciated (e.g., Neuweiler 1984). The Phyllostomidae, the New World tropical and subtropical spear-nosed bats, are unequalled in variety of choices of foods (Gardner 1977) and thus offer a good opportunity to examine the ecology of echolocation call design (Novick 1963). This paper describes prey selection, foraging behavior, and echolocation call characteristics in one subfamily of phyllostomids (the Phyllostominae) that were tape-recorded and observed in the lowland, tropical moist forest of Barro Colorado Island, Lake Gatun, Panama (BCI) (9°9'N, 79°51'W). Fifty-eight species of bats occur on BCI (Handley, personal communication), including 15 phyllostomines that range in size from 6 to 150+ g (Bonaccorso 1979).

Phyllostomines are the most primitive phyllostomids (Smith 1976). Little is known about their foraging habits although as a group, they appear to be omnivorous and feed on insects, fruit, pollen, nectar, and small vertebrates. Members of several genera (Vampyrum, Trachops, Tonatia, Mimon, some Micronycteris) have long ears (see frontispiece) and hover, and are thought to glean prey from foliage, tree trunks, the ground, or other substrates (Hill and Smith 1984). Tuttle and Ryan (1981) confirmed this in Trachops cirrhosus and also showed that these bats use frog calls to locate frogs as prey. Recently, Belwood (this study, Chap. 6) showed that Micronycteris megalotis, M. hirsuta, Tonatia silvicola, and Trachops cirrhosus use similar calls to locate and glean singing insects, specifically katydids.

Materials and Methods

Bats were caught after sunset in mature forest on BCI (Fig. 2-1) with standard 6 or 12 m mist nets. Echolocation calls were recorded, under red light, in a large (4.5 by 4.5 by 2.3 m), unobstructed, outdoor, screen, flight cage using a Racal Store 4D recorder operated at 76 cm/sec, a QMC SM1 broadband microphone (QMC Instruments, Inc., London, England), and NLS Model 15 oscilloscope (Non-Linear Systems Inc., Solana Beach, CA, U.S.A.) (system response 25 Hz to 40 kHz \pm 1.0 dB). At least 2 animals and 20 calls were

recorded for each species and analyzed at 8, 16, or 32 times reduced real tape speed with a Nicolet 100A Fast Fourier Transform (FFT) Mini-Analyzer.

Diets, and various elements of foraging behavior, were determined by analyzing feces from wild caught bats, by conducting feeding experiments in flight cages, and by examining prey remains (mainly culled insect wings) that accumulate in the natural feeding roosts of some of the bats (Belwood this study, Chap. 3). Additional information, when available, was obtained from the literature.

Results

Members of 14 species of phyllostomine bats (162 individuals) were captured at night while foraging. All occurred in dense forest. None were caught in clearings or in other areas without trees. Fecal analyses (Table 4-2) show that insects made up a large portion of the diets of M. megalotis, M. hirsuta, M. brachyotis, M. schmidtorum, Mimom crenulatum, Macrophyllum macrophyllum, Tonatia bidens, T. silvicola, and Trachops cirrhosus. The latter also fed on vertebrates. In captive feeding studies (Belwood this study, Chap. 4), M. nicefori, and Phylloderma stenops refused insects and fed only on fruit pulp and juices, and Chrotopterus auritus accepted only raw meat, in this case chicken. Phyllostomus hastatus and P. discolor fed on both

insect and fruit. In general, the above data confirm what little was previously surmised about phyllostomine food habits (Gardner 1977).

Among the insectivores for which reasonable fecal samples were obtained (T. bidens, T. silvicola, T. cirrhosus, M. megalotis, M. hirsuta; Table 4-2), Orthoptera (katydids, roaches, and crickets) dominated in the diet. At night, in the forest, these insects are stationary, or move along the ground or foliage, at varying speeds, fully exposed (Belwood, personal observation). This indicates that these insects may have been gleaned from these surfaces by the bats. Evidence from captive feedings supports this (Belwood this study, Chap. 4).

Two bat species studied in the lab, T. silvicola and M. hirsuta, gleaned insects from the ground and returned to feeding perches to consume them in a manner similar to that described for certain other Old World gleaning bats [e.g., Cardioderma cor (Megadermatidae) (Vaughan 1976), Nycteris grandis and N. thebaica (Nycteridae) (Fenton, Gaudet and Leonard 1983), and Megaderma lyra (Megadermatidae) (Marimuthu and Neuweiler 1987)]. These two species succeeded only in locating insects that were calling [i.e., katydids; Belwood (this study, Chap. 6)] or were otherwise producing noise (usually as they walked on leaf litter on the ground). Like the Old World gleaners, these bats, when hungry, could not locate a live but silent or non-moving

prey, even when it was only a few cm away (Marimuthu and Neuweiler 1987).

Beetles [10 to 25 mm body length (BL)], also presumably gleaned, followed in importance in the diets of M. hirsuta, M. megalotis, T. bidens, and Trachops cirrhosus. Only M. crenulatum and M. macrophyllum deviated from the Orthoptera-eating trend by feeding on small (5 to 10 mm BL) beetles (76.6%) and moths (size unknown) (100%), respectively. Whether these insects were gleaned by the bats is not known, although the small size of the insects taken by M. macrophyllum suggests that in this species they were not.

Eleven M. hirsuta and 27 M. megalotis roosts containing the remains of 10,944 and 12,055 insects, respectively, were found (Table 5-1). Usually, these roosts served as feeding roosts and day roosts, and were used for months or years at a time by small groups of 5 to 15 individuals, indicating that the bats foraged regularly in small locally familiar feeding territories. Over a two year period, the dominant prey items eaten by the 6 g M. megalotis were roaches (15 to 20 mm BL; 26.0%), scarab beetles (10 mm BL; 27.3%) and dragonflies (35 to 40 mm BL; 14.3%). Katydid (35 to 40 mm BL; 41.1%), scarabs (15 to 20 mm BL; 13.6%), and roaches (20 to 35 mm BL; 10.1%) were fed on most commonly by the 15 g M. hirsuta. Only two T. silvicola feeding roosts were found, each containing the wing remains of a few large

Table 5-1.--Major insect prey (percent by number) of *Micronycteris megalotis* and *M. hirsuta*, two sympatric foliage gleaning phyllostomine bats from Barro Colorado Island, Panama, as revealed by an analysis of the insect remains found in bat roosts.

BAT SPECIES (forearm-mm)	WEIGHT (G)	# OF ROOSTS	# INSECTS EATEN	ROACHES (BL) (*)	SCARABS (BL)	ODONATES (BL)	KATYDIDS (BL)
<u>M. MEGALOTIS</u> (30-34)	6	27	12,055	26.0 (15-20 mm)	27.3 (10 mm)	14.3 (35-40 mm)	1.4 (20-25 mm)
<u>M. HIRSUTA</u> (42-45)	15	11	10,944	10.1 (20-35 mm)	13.6 (15-20 mm)	1.4 (35-45 mm)	41.1 (35-40 mm)

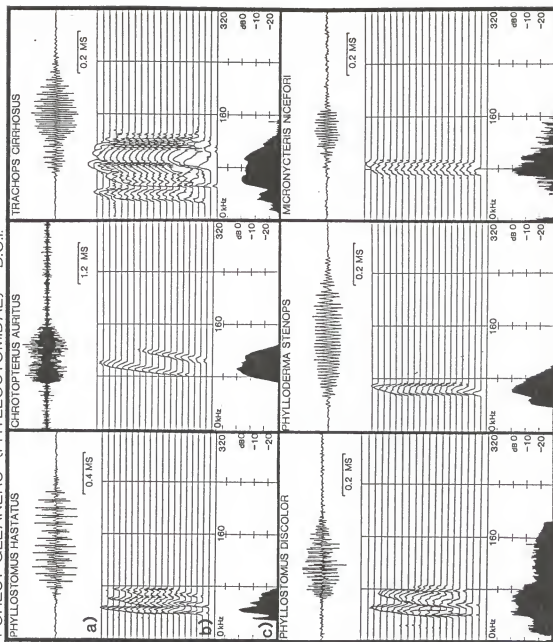
(*) BL = body length in mm

katydid (Acanthodis curvidens; about 45 mm BL). Anne Brooke (Biology Department, University of Tennessee; personal communication) also reports difficulty finding permanent Tonatia roosts in lowland forests in La Selva, Costa Rica, that contain culled insect pieces. This indicates that these bats probably roost (or at least feed) singly, do not use roosts near the ground, or do not use the same roosts day after day, but instead travel to a variety of scattered roosts from which they forage. Tuttle (1970) reports finding T. silvicola roosts in abandoned termite nests in trees.

Oscillograms and FFT analyses of phyllostomine echolocation calls comprise Figs. 5-1 (carnivores and nectarivores) and 5-2 (insectivores). Regardless of diet, the calls of all these bats are remarkably similar; they are 'short' (< 2 msec; Simmons and Stein 1980), low amplitude (Belwood, Fullard and Handley, unpublished data), high frequency, broadband signals with multiple harmonics. They are characteristic of the "high resolution, clutter-rejecting, pursuit strategy" calls described by Simmons, Fenton and O'Farrell (1979). They also resemble the calls of sympatric frugivores and nectarivores in other, mainly frugivorous, phyllostomid subfamilies (the Stenoderminae, Carolliinae) that forage in BCI forests (Howell 1974; Novick 1977; Belwood, Fullard and Handley, unpublished data; Fig. 5-3). In contrast, the calls of insectivorous bats on

Fig. 5-1.--Oscillograms (a) and FFT (sound spectrum) analyses (b and c) of the echolocation calls of nectar feeding and carnivorous foliage gleaning bats (Chiroptera: Phyllostomidae: Phyllostominae) recorded on Barro Colorado Island, Panama. These bats occur in forested areas, and have "high resolution, clutter-rejecting pursuit strategy calls" (Simmons, Fenton and O'Farrell 1979). (c) represents the sound spectrum of the entire call while the sound spectra in (b) are for successive twentieths of the call. (c) is read starting at the top of the figure.

FOREST GLEANERS (PHYLLOSTOMIDAE) - B.C.I.



CARNIVORES

NECTARIVORES

Fig. 5-2.--Oscillograms and FFT (sound spectrum) analyses of the echolocation calls of insect-eating foliage gleaning bats (Chiroptera: Phyllostomidae: Phyllostominae) recorded on Barro Colorado Island, Panama. These bats occur in forested areas, and have "high resolution, clutter-rejecting pursuit strategy calls" (Simmons, Fenton and O'Farrell 1979).

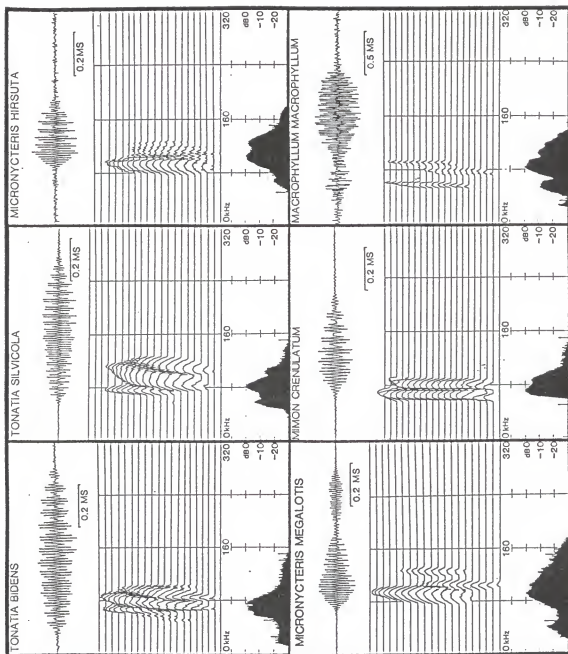
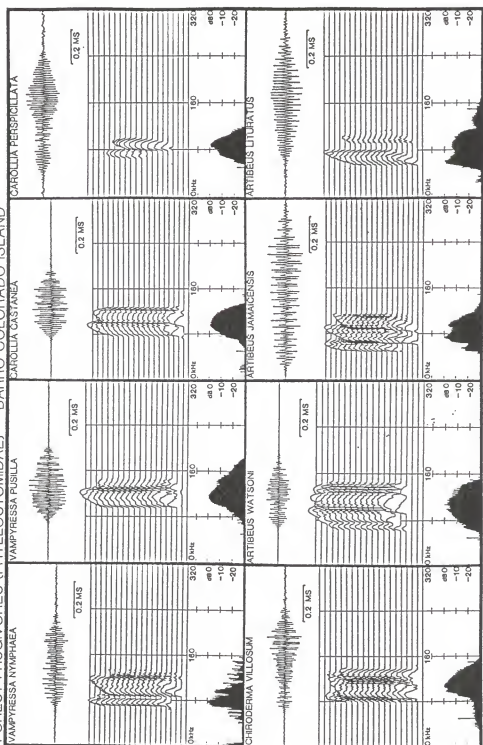


Fig. 5-3.--Oscillograms and FFT (sound spectrum) analyses of the echolocation calls of frugivorous spear nosed bats (Chiroptera: Phyllostomidae: Stenoderminae, Carollinae) recorded on Barro Colorado Island, Panama. These bats occur in forested areas, and have "high resolution, clutter-rejecting pursuit strategy calls" (Simmons, Fenton and O'Farrell 1979).

FOREST FRUGIVORES (PHYLLOSTOMIDAE) — BARRO COLORADO ISLAND



BCI that forage on the wing are much narrower in frequency bandwidths. They are "basic pursuit strategy" calls (Simmons, Fenton and O'Farrell 1979). Aerial insectivores that forage in open spaces [Myotis spp., Rhogeessa tumida (Vespertilionidae) (Fig. 5-4); Molossus spp. (Molossidae), (Simmons, Fenton and O'Farrell 1979 and Simmons and Stein (1980)] have much lower frequency, frequency modulated (FM) signals with shallow to broad sweeps and no harmonics. Echoes from such calls are good estimators of target range (Simmons and Stein 1980), and also give information on target quality. In contrast, the aerial insectivores that forage in open spaces (gaps) under the forest canopy [Pteronotus parnellii, P. gymnotus (Mormoopidae); Saccopteryx leptura (Emballonuridae)] have long, constant frequency (CF) signals that are used for the accurate determination of target (i.e., insect) motion (approach, velocity and direction) against the fixed background of stationary objects (trees) (Fig. 5-5).

Discussion

All the phyllostomine bats in this study forage in a humid, cluttered tropical forest, on prey or food items that are intimately associated with plant substrates or the ground. The same is true for the frugivorous and nectarivorous bats in the other phyllostomine subfamilies

Fig. 5-4.--Oscillograms and FFT (sound spectrum) analyses of insect-eating aerial insectivore bats (Vespertilionidae) that feed in clearings on Barro Colorado Island, Panama. These are "basic pursuit strategy calls" (Simmons, Fenton and O'Farrell 1979).

'CLEARING' AERIAL INSECTIVORES (VESPERTILIONIDAE) B.C.I.

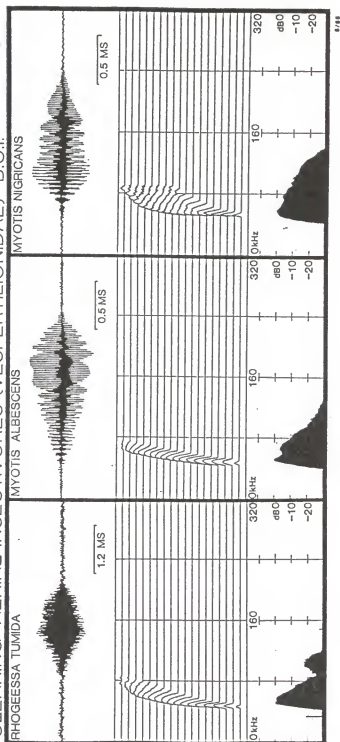
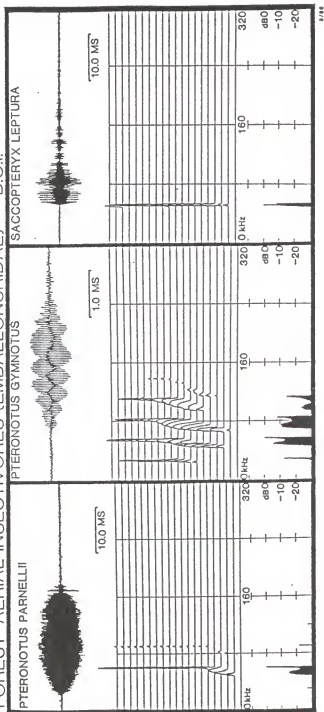


Fig. 5-5.--Oscillograms and FFT (sound spectrum) analyses of the echolocation calls of insect-eating aerial insectivore bats (Mormoopidae, Emballonuridae) that feed under the forest canopy in dense forest on Barro Colorado Island, Panama. These are "velocity-sensing clutter-rejection pursuit strategy calls" (Simmons, Fenton and O'Farrell 1979).

'FOREST' AERIAL INSECTIVORES (EMBALLONURIDAE) — B.C.I.



mentioned above. Clutter-rejection calls appear well suited to this environment as they limit the range of outgoing calls, limit echo information to nearby objects, and decrease pulse-echo overlap (Novick 1977). Compared to narrower band calls, they also provide greater acuity for the perception of obstacle (and target) position and fine structure in the bats' immediate surroundings (Vogler and Neuweiler 1983). This is also adaptive in cluttered habitats. Old World bats [e.g., Nycteris thebaica and N. grandis (Fenton, Gaudet and Leonard 1983), and Megaderma lyra (Megadermatidae; Neuweiler 1984)], and other New World gleaners [Macrotus californicus (Phyllostomidae) (Bell 1985) and M. waterhousii (Belwood, unpublished data)] that glean prey in similar environments also use this type of call.

Other factors that may affect the design of the short calls described here include: 1) the presence of large carnivorous bats (Vampyrum spectrum, C. auritus, P. hastatus) that may use the echolocation calls of other bats to locate the bats that are producing them as prey; 2) the need to avoid acoustical interference with katyids (Orthoptera: Tettigoniidae) that sing intensely (90 to 110 dB at 10 cm), are plentiful in the BCI forest, and emit songs in the 15 to 45 kHz range (Belwood this study, Chap. 7); 3) the hearing acuity of potential tympanate prey--it is probably no coincidence that M. hirsuta, which feed the most heavily on katyids, also have the shortest calls of the

insectivorous phyllostomines recorded here (0.31 ± 0.05 msec., stats; Table 5-2); and 4) the distance the bats travel from day roosts to feeding areas. Small bats such as M. megalotis and M. hirsuta (peak call frequencies 106.8 ± 10.1 and 100.6 ± 10.1 kHz, respectively), forage from their day roosts (as evidenced by the build-up of thousands of insect wings) in familiar areas, and on insects that are abundant and evenly dispersed. In contrast, larger bats such as T. cirrhosus (peak frequency 79 to 53 kHz; Barclay et al. 1981), and perhaps T. silvicola, which feed on prey whose concentrations may be ephemeral and localized (e.g., frogs and larger insects), probably travel greater distances to feeding roosts in search of prey, and thus benefit from lower frequency calls that attenuate less than higher frequency calls. For flying bats, lower frequency sounds increase the distance from which obstacles can be detected (Barclay 1988), which is important if the bats fly great distances and in unfamiliar areas.

The similarity in the calls of phyllostomines (i.e., carnivores, insectivores, and nectarivores) and other phyllostomids (i.e., frugivores) observed here indicates that foraging habitat, rather than diet, may be the main factor determining the basic type of echolocation used by phyllostomine bats. An important question, however, remains to be answered--can echoes from clutter rejection calls in these bats be used to distinguish potential food items

Table 5-2.--Echolocation call characteristics of the insectivorous phyllostomine (Phyllostomidae) bats of Barro Colorado Island, Panama. Figures are means \pm standard deviations. Range values are given in parentheses.

BAT SPECIES	FOREARM (mm)	N(*)	HARMONICS (#)	PEAK FREQ. (kHz)	FREQ. RANGE (kHz)	DURATION (ms)
<u>MICRONYCTERIS MEGALOTIS</u>	30-34	40/3	2.4 \pm 0.7 (1-3)	106.8 \pm 10.1 (86.0-126.8)	69.1 \pm 15.1 (44.4-95.6)	0.6 \pm 0.2 (0.3-1.2)
<u>MICRONYCTERIS HIRSUTA</u>	42-45	22/3	2.0 \pm 0.2 (2-3)	100.6 \pm 10.1 (89.6-125.6)	51.3 \pm 7.6 (35.2-65.6)	0.3 \pm 0.05** (0.2-0.4)
<u>MIMON CRENULATUM</u>	48-52	34/3	1.7 \pm 0.5 (1-2)	71.9 \pm 3.4 (65.2-77.2)	37.1 \pm 4.0 (29.2-44.8)	1.1 \pm 0.3 (0.5-1.9)
<u>TONATIA SILVICOLA</u>	51-53	40/3	2.7 \pm 0.5 (2-3)	79.1 \pm 9.0 (56.4-92.4)	61.2 \pm 10.1 (36.0-76.0)	0.9 \pm 0.2 (0.5-1.4)
<u>TONATIA BIDENS</u>	55-60	40/3	1.8 \pm 0.7 (1-3)	73.8 \pm 6.7 (52.8-87.2)	46.4 \pm 10.0 (23.6-75.2)	0.6 \pm 0.2 (0.3-1.4)

(*) Number of pulses analyzed/Number of individuals

(**) Significantly shorter than calls of other insect-eating species; STATS.

(stationary insects, fruit, flowers, et cetera) from the dense foliage with which the latter are associated? The inability of T. silvicola and M. hirsuta to locate silent prey, in contrast to their responses to calling or noisily walking insects (in screen cages), strongly indicates that they do not (Belwood this study, Chap. 6). Recent evidence for Old World gleaners confirms this (Marimuthu and Neuweiler 1987). As pointed out by Simmons, Fenton and O'Farrell (1979), the precise localization of food by these bats may well result, not from echolocation, but from the exploitation of such prey features as conspicuous odor (in fruits and flowers), sound (in animal prey) (see Fiedler 1979, Bell 1982), or vision (Bell 1985, Bell and Fenton 1986). Along these lines, two other questions deserve attention with respect to the insectivorous phyllostomines--1) Why are moths not preyed on more heavily by the gleaning bats of BCI? Other gleaning phyllostomines [e.g., Macrotus waterhousii in the West Indies, (Belwood, unpublished data)] take moths in large numbers; and 2) how do M. megalotis and M. hirsuta, which have similar echolocation calls, but feed on different-sized insects (Table 5-1), gauge insect size if echolocation is not used to locate prey?

Clearly, much work remains to be done on the ecology of echolocation in bats.

CHAPTER 6
BAT PREDATION AND ITS INFLUENCE ON CALLING BEHAVIOR
IN NEOTROPICAL KATYDID

Introduction

In many animal species, members of one sex use acoustic signals to attract mates. These include male Orthoptera and cicadas (Otte 1977) and frogs and toads (Kiestler 1977). Mate-attracting calling songs are species-specific, unambiguous, and highly localizable, which helps them function successfully in sexual pair formation. These same characteristics, however, reveal the location of calling animals to predators and parasites (Cade 1975; Soper, Shewell and Tyrrell 1976; McKeever 1977; Tuttle and Ryan 1981; Ryan, Tuttle and Taft 1981). In a recent study, Tuttle, Ryan and Belwood (1985) showed that some bats in Panama, Tonatia silvicola and Trachops cirrhosus, responded to tape recordings of male katydids (Orthoptera: Tettigoniidae: Phaneropterinae) with a carrier frequency of 12 kHz.

This report describes field and flight cage experiments with live insects, to show that members of at least four species of New World foliage gleaning bats (FGB) (Phyllostomidae: Phyllostominae) exploit katydid songs as prey-finding cues. It also shows that song duty cycle in

katydids (proportion of time spent singing) is markedly reduced in understory species occurring with FGB (in mature forest), but not in species in areas without FGB (second growth). (FGB pluck insects from stationary surfaces, and consume these from woody perches in dense forest. They are uncommon in areas without large mature trees.) The previously unappreciated occurrence of tremulation signals in forest katydids that offset the information loss of a lowered duty cycle is also reported. These katydids supplement their acoustic cues with complex species-specific body vibrations that are inaudible, but travel through plants to conspecifics. Insectivorous bats and their prey have long co-evolutionary histories, and bats have influenced the development of behavioral and morphological anti-predator adaptations in moths (Roeder 1967), green lacewings, (Miller 1975), crickets (Moiseff, Pollack and Hoy 1978), and mantids (Yager and Hoy 1986). The findings presented here represent the first report of widespread behavioral anti-bat defenses in katydids, another large group of insects.

Materials and Methods

Mist nets were baited with singing male katydids to demonstrate that bats respond to song cues. Two 6-m nets were set at ground level, 3 m apart within 30 m of a known

or suspected FGB roost, in forested areas ('Mature Forest', Fig. 2-1) on BCI for one hour beginning at sunset on 13 evenings between January and March 1984. One was 'baited' with a singing male katydid [Ischnomela pulchripennis or Scopiorinus fragilis (Tettigoniidae: Pseudophyllinae); carrier frequencies about 14.6 and 25.2 kHz, respectively, (Belwood this study, Chap. 7)] in a cylindrical screen cage (30 by 18 cm) supported on a meter stick 10 cm from the net, the other (control) with a conspecific female.

In order to determine diet, prey remains (culled, sexually dimorphic whole insect wings) that accumulated in natural FGB roosts (Belwood this study, Chap. 3) were collected bi-weekly from 38 sites between January 1983 and December 1984.

To explore the influence of FGB predation on katydid call design, calling songs were recorded and analyzed from members of 17 forest-dwelling katydid species (Belwood this study, Chap. 7) and were compared to the calls from members of four dominant clearing species. Three katydids of each species were recorded individually, at 25-27°C, under red light with a Nagra IV-SJS tape recorder (operated at 38 cm per second) (Kudelski, S.A., Lausanne, Switzerland) and a B&K one-quarter inch condenser microphone (Bruel and Kjaer Instruments Inc., Marlborough, MA, U.S.A.) (system frequency response 25 Hz to 40 kHz \pm 1.0 dB) (Belwood this study,

Fig. 7-1). Calls were analyzed with a Uniscan II (Multigon Industries Inc., Mt. Vernon, NY, U.S.A.) audiospectrograph.

To determine the potential selective advantage of 'inconspicuous' katydid calls the average response times of T. silvicola to katydids producing 'frequent' (60 calls per min) and 'infrequent' (< 1 call per min) calls, respectively, were compared. Five unfed T. silvicola were tested in a red lit screen flight cage (4.5 by 4.5 by 2.3 m) (Fig. 6-1). A bat (Fig. 6-2a) perched in one corner of the cage and was observed from the opposite corner. A male katydid (S. fragilis, about 60 calls per min, carrier frequency 25.2 kHz, or Acanthodis curvidens (Pseudophyllinae), < 1 call per minute, carrier frequency 13 to 16.8 kHz) in a screen cage (18 by 30 cm) (Fig. 6-2b), and a control cage containing an equal size female, were placed on the floor in the remaining corners, 4 m from the bat. Trials began when the male began to sing, and ended when the bat landed on, or within 10 cm of, a cage. Correct choices were not rewarded. Position of the singing insect was changed randomly after each trial. Trials were repeated every 15 to 30 min, when the insect resumed singing. The same bats were tested for seven trials each with frequently and infrequently calling katydids. Only one category of calling insect was tested each night. Female katydids were never approached.

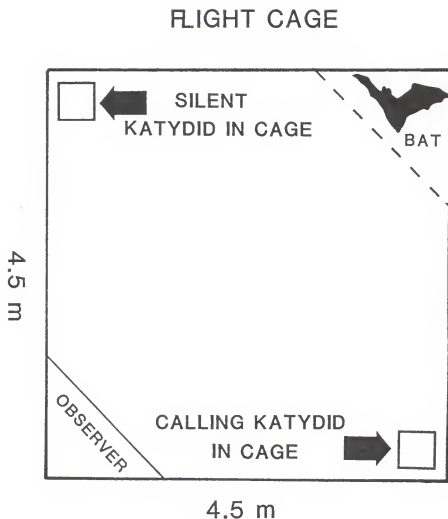


Fig. 6-1.--Schematic diagram of flight cage set-up used to test phonotactic responses of bats, Tonatia silvicola, to katydid calls. See text for explanation.



Fig. 6-2.--Bat (a) perched in large flight cage, and caged katydid (b) in flight cage used in bat phonotaxis experiment.

Tremulations were recorded from katydids in wooden cages (40 by 40 by 30 cm) in which one side consisted of a loose glass panel. Each tremulation rattled the glass once, producing an audible sound that was recorded with a Sony Walkman recorder whose microphone was placed on the glass (Belwood this study, Chap. 7). Tremulation patterns were analyzed with a Uniscan II audiospectrograph. Females were also observed to tremulate. However, their tremulations were fainter than those of males, so that they could not be recorded in this manner.

Results and Discussion

Members of four FGB species (six Micronycteris megalotis, eight M. hirsuta, nine T. silvicola, one Trachops cirrhosus) responded to the calls and were caught in nets (Table 6-1). FGB were not attracted to control nets baited with silent females ($X^2 = 24$; $P < 0.001$). 1.85 FGB per net hour were captured in male-baited nets. In contrast, Bonaccorso (1979) netted 0.017 FGB per net hour in unbaited nets in 5177 hours on BCI. Ten frugivorous bats (Artibeus spp., Carollia spp., Centurio senex) were also caught in male-baited nets, and 14 in the controls.

Analysis of prey remains showed that at least one species fed heavily on katydids; 41.1%, by number, and 61.5% by weight, of 10,944 insects found in 11 M. hirsuta feeding

Table 6-1. Bats caught in mist nets on Barro Colorado Island, Panama, that were baited with singing male katydids.

BAT	^a DIET	EXP. NET (Singing Male)	CONTROL NET (Silent female)
<u>Artibeus</u> spp.	Fruit	b 9	b 7
<u>Carollia</u> spp.	Fruit	b 1	b 6
<u>Centurio</u> <u>senex</u>	Fruit	0	1

<u>Micronycteris</u> <u>megalogotis</u>	Insects (FG)	6	0
<u>Micronycteris</u> <u>hirsuta</u>	Insects (FG)	8	0
<u>Tonatia</u> <u>silvicola</u>	Insects (FG)	9	0
<u>Trachops</u> <u>citrhorus</u>	Frogs/Insects (FG)	1	0

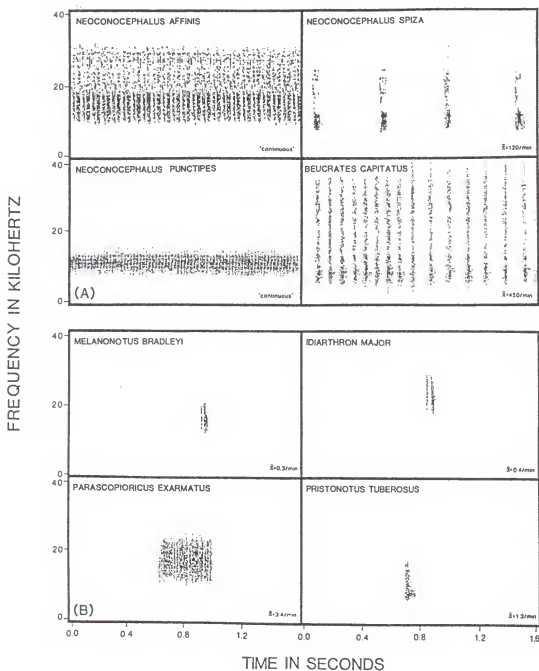
^a FG = Foliage Gleaner	^b excludes bats attracted by distress calls of other bats		

roosts were katydids (Belwood this study, Chap. 4). Although they do not call, at least 50% of the katydids consumed that could be sexed were female. How these were located by the bats is not known.

Katydid from clearings signal with 'conspicuous' calls; they have broad-band carrier frequencies, in or near the upper audio range, and relatively high duty cycle (little down time) (Fig. 6-3a). Conversely, calls from forest forms have sinusoidal frequencies (purer tones) in the high audio or ultrasonic range and remarkably low duty cycle (Fig. 6-3b), attributes that make them difficult for mammalian ears to locate (Marler 1955). Rentz (1975) and Morris and Beier (1982) noted little acoustical activity in Costa Rican rainforest katydids and hypothesized that this was a response to bat predation pressure. Only one forest katydid in this study, Ischnomela pulchripennis, has 'localizable' call features such as those found in clearing katydids (Belwood this study, Chap. 7). It sings from large (2 m) terrestrial bromeliads (Aechmea magdalenae), that are covered with long, sharp spines that could injure a bat's delicate wings. It is not taken as prey. In contrast, the other forest katydids observed called fully exposed from understory-plant leaf surfaces.

Bats located frequent calls in 26 ± 11 s (mean \pm standard error; $n = 35$), and flew directly to the insect producing the sound. Infrequent calls took significantly

Fig. 6-3.--Audiospectrograms (a) of airborne calling songs of members of four dominant clearing katydid species (Orthoptera: Tettigoniidae) on Barro Colorado Island, Panama (BCI). These insects are not preyed on by bats. Their calls emphasize lower frequencies, are broadband, and are produced frequently. Airborne calling songs (b) of members of four forest-inhabiting katydid species on BCI. These calls are short, infrequent, and relatively high and pure in tone, making them difficult for mammalian ears to localize. They typify katydid songs in areas inhabited by tropical New World foliage gleaning bats (Phyllostomidae: Phyllostominae). X = average call repetition rate per minute for 3 to 5 individuals.



longer to locate (34 ± 11 min; $n = 35$; $U = 1225$, $t = 7.20$; $P < 0.0005$), because responding bats made repeated short, erratic flights lasting only as long as the insects' calls. The bats did not locate silent insects.

S. fragilis and A. curvidens calls differ in carrier frequency. Therefore, response times to different repetition rates are not really comparable. Both calls, however, elicited immediate flight indicating that they were perceived by the bats. Also, in a previous study (Tuttle, Ryan and Belwood 1985) T. silvicola consistently responded to recordings of a 'frequent' 12 kHz katydid call in less than one minute.

Reduced song production in katydids was unexpected since worldwide, these animals are considered among the most acoustically active of insects. Moreover, short inconspicuous calls increase localization difficulties for attracted females. So, it is not surprising that forest katydids supplemented their songs with another type of communication, in the form of complex and vigorous body vibrations (tremulations) that are strong enough to visibly shake plants, but are inaudible and travel through plants to other individuals (Belwood this study, Chap. 7). These were originally described in a Costa Rican katydid by Morris (1980), who also suggested their role in reducing bat predation. Tremulations appear more energetically costly to

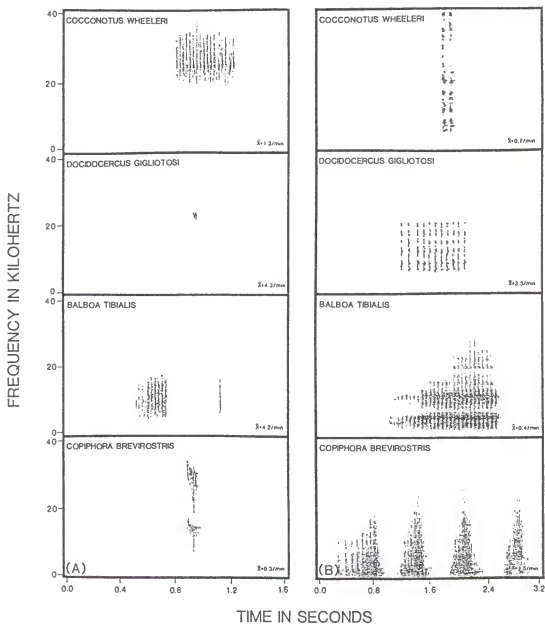
produce than short airborne calls, but do not appear to be perceived by FGB.

Tremulations were observed in 13 species of forest-katydids [Acanthodis curvidens, Balboa tibialis, Cocconotus wheeleri, Docidocercus gigliotosi, Eucocconotus camerani, Idiarthron major, Ischnomela gracialis, I. pulchripennis, Melanonotus bradleyi, Pristonotus tuberosus, Xestoptera cornea (all Pseudophyllinae); Copiphora brevirostris, Copiphora sp. (Copiphorinae)] and recorded from males of six (Belwood this study, Chap. 7). The vibrations are structured, stereotypically amplitude modulated, species-specific (Fig. 6-4b), and produced only at night, between (but not during) the short acoustic calls. Isolated males in cages produced tremulations in the absence of females. Females near conspecific males answered with tremulations of their own, leading males to tremulate more often and to cease audible calling. Alone, two individual B. tibialis males tremulated 1.86 ± 2.18 per 5 min period ($n = 24$). An answering female, in a separate opaque cage 1 m from the male on the same wooden bench, increased male tremulation production to 12.25 ± 3.09 per 5 min period ($n = 24$, $U = 569$, $t = 5.83$, $P < 0.0005$). Males also produced 21.42 ± 13.34 airborne calls per 5 min period without an answering female ($n = 24$), and no airborne calls when a tremulating female answered. Males and females in separate opaque cages on the same wooden bench communicated

Fig. 6-4.--Patterned, species-specific, male produced airborne (a) and substrateborne (b) calling songs of members of four forest katydid species on Barro Colorado Island, Panama. (Tremulations were also recorded from Acanthodis curvidens and Eucocconotus camerani.) Individual tremulation pulses in the last three pulse sequences of Copiphora brevirostris occur too rapidly to be differentiated by the recording method used (see text). However, they can be seen in the first pulse sequence. N.B., tremulations are not audible; the spectral component of the patterns is an artifact of the atypical substrate used to record the signals. Also, the time scales differ for the two types of signals.

AIRBORNE CALL

TREMULATION



with one another in this fashion for several hours even when separated by distances of 2.5 m.

With the exception of the insects described here, vibrations in katydids, when they occur, are produced only after individuals come together as a result of acoustic signalling (Busnel, Pasquinelly and Dumortier 1955; Gwynne 1977) or, as simultaneous but weak by-products of stridulation (song production) that aid neurologically in species-specific song coding (Kalmring, Lewis and Eichendorf 1978; Kalmring and Kuhne 1980; Gogala 1985). Tremulations in the katydids described here are temporally distinct from stridulation and are produced in the absence of females. They appear to have developed to supplement reduced audible outputs. Their duration and intensity suggest that they are more energetically costly to produce than the airborne calls. They are analagous to the cues used by some spiders to attract mates (Rovner and Barth 1981), and should function at long range through the substrate since katydids have sensitive vibration receptors (subgenual organs) (Hutchings and Lewis 1983).

Predation on sexually signalling males is an important mortality factor (Burk 1981), and bat predation has influenced the evolution of calling in animals such as neotropical frogs (Tuttle and Ryan 1981). Because FGB eat large numbers of katydids, respond to their airborne calling songs, and have considerable difficulty in locating sporadic

callers, it is reasonable to suggest that they have also influenced calling song design in these insects. Signals that are transmitted through substrate, and as such do not compromise the vital process of mating, are adaptive in the presence of acoustically orienting predators. This refutes the notion of the exclusive role of acoustic song in katydid pair formation.

How the FGB located the large number of female katydids eaten is not known. These bats appear to use passive (prey-produced) sound rather than echolocation to locate prey (Belwood this study, Chaps. 5 and 6). Most female Orthoptera search for and locate singing males and thus spend more time moving in the open exposed to bats. They may risk potential predation merely as a result of responding to calling males (Sakaluk and Belwood 1984). The implications of this selection pressure for the evolution of female katydid behavior are great both in terms of anti-predator defences and in the choice of calling males, but the effects of such predation are unknown.

CHAPTER 7
SEXUAL ADVERTISEMENT IN THE RAINFOREST KATYDIDS
OF LOWLAND PANAMA

Introduction

Worldwide, katydids (Insecta: Orthoptera: Tettigoniidae) number about 3000 species (D.A. Nickle, personal communication) and are a dominant component of the nocturnal insect faunas of both the Old and New World tropics. These insects resemble grasshoppers in overall body shape, and many, primarily the Phaneropterinae and some Pseudophyllinae, are famous for their leaf-like appearances (Cott 1957; Robinson 1969a; Edmunds 1974; Nickle 1988; Morris, Klimas and Nickle, in press).

In many katydid species, males produce species-specific calling songs in order to attract conspecific females with which to mate (Otte 1977, Gwynne and Morris 1983, Kalmring and Elsner 1985). These acoustic calls (calling songs) are produced with specialized structures (file and scraper) at the bases of the forewings. Sound is produced when the scraper on the right wing impacts each tooth on the file of the left wing, which causes a specialized structure on the latter (the mirror) to vibrate (Michelsen and Nocke 1974, Sales and Pye 1974).

In the simplest scenarios males, which often occur in groups (Greenfield and Shaw 1983), produce their calls; females, which are silent, perceive these and approach the conspecific callers of their choice. In theory, selection should enhance characteristics of the signal that promote effective long distance propagation and localizability of the signal by females. These insects, along with crickets, have been used extensively as models to describe acoustical pair formation in insects [e.g., Dumortier (1963c); Sales and Pye (1974); Gwynne (1977); Morris, Kerr and Gwynne (1975); Morris, Kerr and Fullard (1978); Feaver (1983); Bailey (1985)].

Several variations on this theme exist. In phaneropterine katydids for example, females respond to male calls with short calls of their own (Spooner 1964, 1968; Nickle 1976) and males and females move toward one another. The female calls are produced by actions involving pegs on several veins of the forewing, which are moved across pegs on the opposite wing (Nickle and Carlysle 1975).

In some New World tropical forest pseudophyllines, the calls of males are short, relatively high in frequency, and are produced sporadically (Morris 1980; Morris and Beier 1982; Belwood this study, Chaps. 6 and 7; Morris, Klimas and Nickle, in press). This appears to be an adaptation against predation by nocturnal acoustically orienting predators, specifically foliage gleaning spear-nosed bats (Chiroptera:

Phyllostomidae: Phyllostominae), that can use katydid calls to locate their prey (Belwood this study, Chap. 6). In practice, shortened calls increase localization difficulties for bats attracted to katydid calls (*ibid.*). In theory, this should also be true for female katydids attracted to male calls.

In apparent response to this, song structure and ear morphology in these katydids appear designed to maximize localization of the short, sporadic airborne call (Morris, Klimas and Nickle, in press). In addition, male pseudophyllines supplement their shortened calls with species specific body vibrations that travel through substrates to other katydids. These are called tremulations and are rapid, short duration, vertical oscillations of the entire body, which are performed perpendicular to the plane of the substratum (Morris 1980). According to Morris (*ibid.*), who reviewed the occurrence of substrate signalling in Ensiferan Orthoptera (katydids and crickets), tremulation on vegetation imparts forces to a plant through the insect's feet. In turn, these forces are propagated as waves along various plant parts (stem, leaf, and petiole). Further discussions of vibrational communication in insects can be found in Gogala (1985); Kalmring (1985); Keuper et al. (1985); and Kalmring and Elsner (1985).

Although the function of tremulation has not been studied in detail, it has been observed as a regular part of

courtship in at least four species (Belwood, unpublished data). In the laboratory, female pseudophyllines respond to conspecific male tremulations with tremulations of their own, and tremulation between males and females can last for over an hour prior to copulation. This is analogous to the way phaneropterine females respond acoustically to the acoustic calls of conspecific males.

The physical structure of calling songs has been described in fewer than one percent of the pseudophylline katydids that are known taxonomically (Morris, Klimas and Nickle, in press). This paper describes the calls of 15 species collected in a lowland Panamanian rain forest. Also included are the calls of two copiphorine species that occur in this habitat.

Materials and Methods

Collecting Specimens

This study was conducted at the Smithsonian Tropical Research Institute's field station on Barro Colorado Island, Lake Gatun, Republic of Panama (BCI; Fig. 2-1). The 17 species studied are listed in Table 7-1 and all were obtained between January 1983 and December 1984.

The majority of study animals was collected in the forest understory. These were located visually, with the aid of a strong flashlight, by walking along established

Table 7-1.--Katyids (Insecta: Orthoptera: Tettigoniidae) from Barro Colorado Island, Lake Gatun, Republic of Panama, whose sexual advertisement signals are discussed in this paper.

SUBFAMILY	SPECIES	AVERAGE BODY LENGTH (mm) (♀)	AVERAGE BODY LENGTH (mm) (♂)
Copiphorinae	<u>Copiphora breviostris</u>	44.4	42.8
Copiphorinae	<u>Copiphora</u> nr <u>breviostris</u>	42.6	37.0
Pseudophyllinae	<u>Acanthodis curvidens</u> (Stal)	49.8	43.5
"	<u>Balboa tibialis</u> (B. von Wattenwyl)	46.4	44.0
"	<u>Coccoconotus wheeleri</u> Hebard	38.4	37.1
"	<u>Docidocercus gigliotosi</u> (Griffini)	37.9	36.4
"	<u>Eucoccoconotus camerani</u> (Griffini)	46.6	53.5
"	<u>Idiarthron major</u> Hebard	42.5	42.7
"	<u>Ischnomela pulchripennis</u> Rehn	44.3	50.2
"	<u>Melanonotus bradlevi</u> (*)	43.8	34.4
"	<u>Mimetica mortuifolia</u>	53.2	35.7
"	<u>Parascopioricus exarmatus</u> Author	35.5	27.3
"	<u>Pristonotus tuberosus</u> (Stal)	61.2	57.1
"	<u>Scopiorinus fragilis</u> (Hebard)	32.0	33.7
"	Unknown pseudophylline "a"	37.9	40.0
"	Unknown pseudophylline "b"	27.3	25.4
"	<u>Xestoptera cornea</u> B. von Wattenwyl	34.8	34.5

(*) discussed in Chapter 6

trails on BCI or in dense forest. This was done for several hours at a time at night, at varying times between dusk and dawn.

Most of BCI's forest katydids are large (> 25 cm in total length) and could be seen from distances of up to 3 or 4 m as they sat fully exposed on the surface of broadleaf plants, stems, lianas or the trunks of trees. Many have long paired antennae (several times body length), which are held out in front of their bodies and are usually the first part of a katydid to be spotted. The eyes of these insects do not shine when illuminated.

Adults or last instar nymphs were also collected at ultraviolet lights operated from dusk to dawn next to the forest edge in BCI's laboratory clearing. Others were collected at incandescent lights on buildings. Four species of "clearing katydids", Neoconocephalus affinis, N. punctipes, N. spiza, and Bucrates capitatus (all Copiphorinae) occurred only in patches of tall grass that grow by buildings. These were not included in the study.

With one exception, the forest katydids studied produced only short, sporadic, high frequency calls. As a result, they were virtually impossible to locate in dense vegetation by their calling songs. This was true even when calling katydids seemed less than a meter from an observer. I. pulchripennis, the exception, sang from within dense clumps of Aechmea magdalenae, a large (> 2 m tall)

terrestrial bromeliad that is covered with long sharp spines. Several specimens were collected from these plants.

In general, forest katydids were collected either by hand (i.e., they were grabbed lightly with the thumb and forefinger in the region of the prothorax), by placing a large vial over their bodies, or with a long (up to 2.5 m) handled insect net. The insects collected in this manner represent species that commonly occurred in vegetation up to about 3 m above the forest floor. When time permitted, the height of the insect above ground level was measured at the time of collection with a rigid poly-vinyl-chloride (PVC) pipe marked at 10 cm intervals to a height of 300 cm. Some pseudophyllines were also found during the day as they roosted in unfurling Heliconia leaves (0.5 to 1.0 m above ground level), or in curled dead leaves ('aerial leaf litter' sensu Gradwohl and Greenberg 1982) that hang from live trees. All field collected katydids were transported to the laboratory in clear plastic bags.

Maintaining Specimens in the Laboratory

All katydids were individually housed in separate screen cages (at least 30 by 30 by 45 cm) that were placed in one of two large screened insectaries. All were subjected to natural photoperiod only (approximately 12 h light: 12 h dark).

Each katydid cage was supplied with a leaf litter substrate, a live potted plant, twigs of various sizes, small slabs of tree bark on which to perch, and several curled dead leaves affixed to the twigs. They were fed small pieces of apple and lettuce daily. Species that were believed to be carnivorous, as evidenced by large mandibles, were also given insects (small flies, cicadas, moths or beetles) as food. As a rule, phaneropterine katydids did not live for more than a few days (the reasons for this are not known), but pseudophyllines could be kept several weeks to several months with no apparent ill effects as long as they were protected from marauding army ants and the stray coati mundis that periodically wandered into the laboratory and attacked insect cages.

Recording and Analyzing Airborne Songs

All calls were recorded in Panama, at night under red light or in complete darkness, at ambient temperature (24 to 27°C), in one of two large screened insectaries. Each had a concrete floor that reduced vibrations caused by people walking near the recording area. Males were recorded alone, (in the absence of responding females) with a calibrated Nagra IV-SJS (Kudelski, S.A., Lausanne, Switzerland) tape recorder operated at 15 ips and a B&K (Brüel and Kjær Instruments, Inc. Marlborough, MA., U.S.A.) 1/4-inch condenser microphone that was placed 10-12 cm from the

insect's cage. The total frequency response of the recording system was 25 Hz to 40 kHz \pm 1.0 dB. Most katydid calls were short, sporadic, high pitched, and thus difficult to hear. Therefore, they were monitored simultaneously with the aid of headphones and a small oscilloscope (NLS Model MS-15; Non-Linear Systems, Inc., Solana Beach, CA, U.S.A.), both of which were connected to the tape recorder. Using this set-up, calls could be monitored even when the tape recorder was not actually in a recording mode.

The individual katydids to be recorded were placed in small cylindrical (10 by 20 cm) fiberglass screen cages. These were insulated on three sides by thick slabs of foam to reduce the recording of sounds reflected from objects around the cage, in a manner similar to that pictured in Fig. 7-1a.

It soon became apparent that most of the katydids studied were very sensitive to the movements (particularly vibrations) of an observer. Therefore, the insect to be recorded was placed in the recording set-up several hours prior to dark. Each insect's singing pattern was monitored for at least one hour and timed with a stopwatch prior to recording. This was done because call production was sporadic and unpredictable, and this procedure minimized the waste of expensive magnetic recording tape and the need to

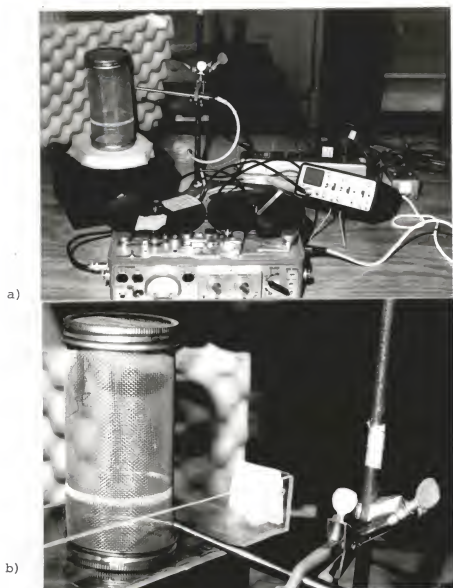


Fig.7-1.-- Equipment used to record the airborne (a) and substrateborne (b) calling songs of katydids (Orthoptera: Tettigoniidae) on Barro Colorado Island, Panama.

change tape reels frequently, and disturb the insect under observation once it had begun to sing.

Slowed tapes of the recorded calls were analyzed with a Nicolet 100A Fast Fourier Transform (FFT) Mini-Analyzer (for spectral analysis), with a Uniscan-II (Multigon Industries, Inc., Mt. Vernon, NY, U.S.A.) (for sonographic analysis), and with a Honeywell Model 1858 Visicorder (Honeywell, Denver, CO, U.S.A.) (for oscillographic analysis).

Song structure in katydids is difficult to describe because individual sound pulses cannot always be delineated without greatly expanding the time frames of the signal. Such an analysis was not possible here. Therefore, the descriptions provided for each song are based on the level of analysis possible and are to be considered relative to the other songs included in the study. [The most serious ramification of this is that what are called "pulses" here (see below) may actually be "pulse trains".] The analyses provided are tentative, pending re-analysis with more sophisticated equipment. The terminology used below follows that of Morris and Walker (1976:792-798), and Morris, Klimas and Nickle (in press):

1. Pulse-the simplest element of amplitude that is easily recognized. This is isolated from other pulses in time by a return to baseline amplitude (i.e., silence).

- a) Rapid decay pulse-a pulse that is characterized by a transient (abrupt) onset, a complex wave form, and a rapid decay after a short duration at maximum amplitude.
- b) Prolonged pulse-a sound wave train characterized by a more gradual onset and a sinusoidal waveform. This is sustained for several to many cycles at approximately peak amplitude.
2. Pulse train-a first order grouping of two or more pulses. These are usually similar and are produced regularly. They are separated by silent intervals that are longer than the silent intervals between pulses in the pulse train.
3. Pulse train group-a second order grouping of pulses; a sequence of two or more mutually distinctive pulse trains.
4. Mode-two or more pulse train groups in succession.
5. Refrain-extremely faint sound emission; less than one-tenth the amplitude of the signal it accompanies.
6. Duty cycle-the percentage of the calling period during which sound is emitted.

The following descriptive terms were also taken from Morris, Klimas, and Nickle (in press):

1. Tick-a noisy (broadband) sound of < 1 s duration whose innerstructure, if any, cannot be resolved by the listener.
2. Zip-a noisy sound of < 1 s duration, with a beady or "serrate" quality, resulting from the listener's perception of pulse structure within the signal.
3. Buzz-a noisy sound sustained for > 1 s that offers no impression of internal pulse or pulse train structure.
4. Rattle-as above, except that repetition rate of the pulse and/or pulse train structure is low enough to be perceived as an effect on the quality of the sound.

Recording and Analyzing Tremulation Calls

Tremulations appear as a rapid succession(s) of vertical oscillations of the abdomen performed when the insect's six legs are firmly planted on the substrate. In large bodied insects, the abdomen may occasionally touch the substrate, but this is usually not the case.

Male katydids that were observed to tremulate did so in whatever cage was used to house them. Although tremulation itself did not produce audible sound, in most cases the vibrations observed were strong enough to shake the insect's cage, or parts of it, which in turn produced an audible tapping sound. This could be enhanced by placing the cylindrical cages in Mason jar lids. (The tops and bottoms of the cages were usually just stapled screen.) Thus,

tremulation could be recorded indirectly by placing a microphone on the insect's cage or on the substrate on which a cage was located (as in Fig. 7-1b). This was connected to a recording Sony Walkman. Like airborne calls, tremulation production was also observed for one hour intervals under red light and counted.

Temporal patterns of the tremulation signals were analyzed by running slowed tape recordings of the recorded sounds through the Uniscan II sound spectrograph to make "sonagrams" of the indirect sounds produced when the insects tremulated. Direct tremulation recordings were also made (courtesy of Dr. G.K. Morris), from plants on which males of two species (C. brevisrostris and D. gigliotosi) were sitting, using a B&K Model 4125 Accelerometer. When placed on a surface, this device transduces changes in vertical displacement such that they can be recorded on magnetic tape for analysis. Tremulation oscillograms for these two species are included here (Figs. 7-7e and 7-9e) to show that the temporal patterns produced by both the indirect (cage noise) and direct (accelerometer) methods are similar, and that the indirect method, albeit crude, successfully reproduces the relative differences in species specific tremulation patterns.

Tremulation was observed in some female pseudophyllines and occurred only in response to tremulations by males. This was observed when males and females were placed toge-

ther or when the insects were in individual cages separated by an opaque barrier on the same wooden bench. In most cases, the female tremulations observed were fainter than those of males, and with only one exception, B. tibialis, could not be recorded in the manner described above.

The terminology used to describe tremulation behavior is as follows (see Fig. 7-2) and differs somewhat from that of Morris (1980):

1. Bounce-the simplest tremulation unit; corresponds to a single body movement (vertical body oscillation), where the body simply moves up once and then down once (Fig. 7-2a).
2. Bounce train-a first order grouping of bounces. A series of two or more bounces produced at regular intervals, and with no major gaps (Fig. 7-2b).
3. Bounce train group-a first order grouping of bounce trains; bounce trains are separated from one another by regular intervals that are longer than those separating the bounces in a train (7-2c). The unit when two or more bounce trains occur together.
4. Tremulation bout-the entire substrateborne call that is produced at varying intervals between airborne calls. Depending on species, this can be a single or double bounce (e.g., Fig. 7-6e), a single long or short bounce train

a) bounce



b) bounce train



c) bounce train group



Fig.7-2.--Schematic representation of terms used to describe tremulation in katydids. An upward-pointing arrow (↑) indicates that the body moves up, a downward-pointing arrow (↓) indicates that it moves down.

(e.g. Figs. 7-5e,f; 7-9d), or one or several bounce train groups (Fig. 7-7d).

The number of katydids recorded and the number of times they sang or tremulated per hour varies with species, and is reported separately for each taxon. For most species, two or more specimens were recorded. Care was taken to observe katydids from any one species sing and tremulate at approximately the same temperatures, i.e., to within 1°C of the values reported in each of the species accounts below. The song parameter values presented are averages (\pm standard deviations) and the number of individuals examined is recorded in each case.

Measurements

The following body measurements were recorded for males and females of each species (see Fig. 7-3); all measurements were taken in mm from live adults that were chilled to reduce body movement. All values are averages (\pm standard deviations):

1. Total Length (TL) (Fig. 7-3a): the linear distance between the frons and the tip of the hind wings (or the tip of the abdomen, if the wings do not cover the abdomen), excluding ovipositor on females, if the latter exceeds the hind wings. This measurement is taken with the wings closed.

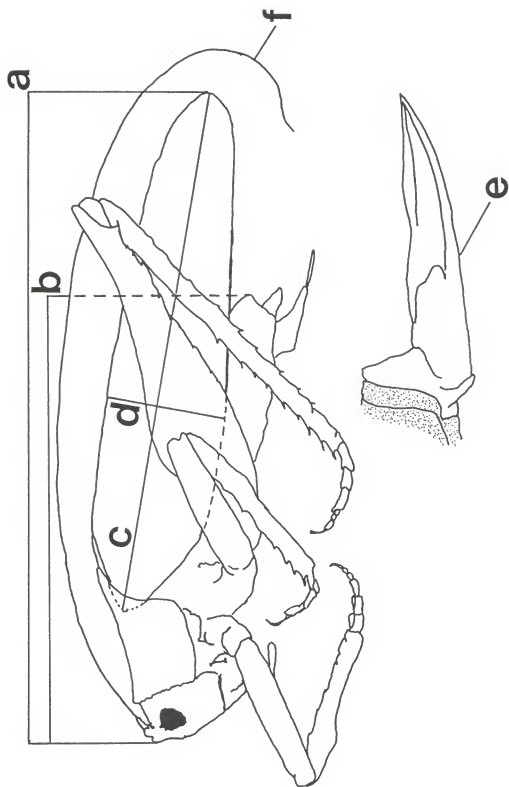


Fig. 7-3.--Measurements taken on the katydids from Barro Colorado Island that are discussed here. These are (in mm): total length (TL) (a), body length (BL) (b), length of left forewing (LLFW) (c), width of left forewing (WLFW) (d), ovipositor (OVIP) (e), and antenna (ANT) (f).

2. Body Length (BL) (Fig. 7-3b): the linear distance between the frons and the tip of the abdomen, excluding cerci and ovipositor.
3. Length of Left Fore Wing (LLFW) (Fig. 7-3c): the greatest linear distance on the fore wing, between its point of articulation with the thorax and apex.
4. Width of Left Fore Wing (WLFW) (Fig. 7-3d): linear distance between costal and anal margins taken at midpoint of wing.
5. Ovipositor Length (in females) (OVIP) (Fig. 7-3e): the linear distance from base to apex of ovipositor.
6. Antennae (ANT) (Fig. 7-3f): the greatest linear length, from the base of the scape to the tip, when the antennae are fully extended. The last measurement is the most variable, as the antennae are often broken (or absent) on field collected specimens.
7. Live Weight (WT): in grams.

Results

Results are presented separately for each taxon studied.

All descriptions refer to live adults. Physical descriptions permit field identification of individuals, but

are less reliable for preserved specimens due to the color deterioration that occurs in dried insects.

The relative abundance categories are as follows:

Rare: only one or two collected during the two year study.

Uncommon: species rarely encountered; fewer than 10 to 15 adults encountered during the two year study.

Common: encountered regularly (one a week or less) on collecting forays when "in season" (i.e., during the season when the adults occur).

Abundant: at least one individual encountered almost nightly when in season.

A considerable amount of additional ecological and behavioral information, albeit anecdotal is also presented for each taxon where known. This is included because there is a paucity of information about the biology of most tropical New World katyids. With the exception of Robinson (1969b) and the scant information in Hebard (1927), virtually nothing is known about the ecology and behavior of Barro Colorado Island's forest katydid species although Walker and Greenfield (1983) and Greenfield (1983, 1988) describe the acoustics and behavior of some of BCI's 'clearing' species.

With respect to calling behavior (i.e., the production of airborne and substrateborne signals), several generaliz-

ations can be made for the katydids studied. At least one male of each species collected sang in captivity. This was usually observed only after the insects had been in captivity for several days.

The insects sang and tremulated in a variety of containers and cages, but sang more readily in larger ones, i.e., ones in which their antennae, which are several times body length in most species, did not touch the sides of their cages. When the insects were large, or had exceptionally long antennae, the latter were cut to body length and this appeared to hasten call production. All individuals were extremely sensitive to vibration and stopped call production (airborne or substrateborne) if an observer or other organism accidentally touched its cage, walked within 5 m of it, or dropped an object on the floor in the room where recording was done. If, for example, a door was slammed in the building next to where recording took place, calling was terminated.

All katydids, are believed to produce faint vibrations that can be transmitted to other organisms via the substrate when they stridulate (produce airborne sounds with the wings) (Keuper et al. 1985). Females use these in conjunction with airborne calls to locate singing males (Latimer and Schatral 1983). The tremulations discussed here in detail differ from those produced during stridulation because they occur completely independent of airborne calls.

In the katydids described below, the production of airborne and substrateborne signals were separate events that occurred in seemingly random alternating fashion within the same block of time. In the absence of females, tremulations were usually produced by males between airborne calls. When sexually receptive females were placed near calling males (i.e., on the same substrates), they responded with tremulations of their own. This usually resulted in an accelerated tremulation rate in the male. The tremulation rates given in the species accounts below are "baseline" values--those that occurred in the absence of females.

Species Accounts

Acanthodis curvidens (Stål)
Pseudophyllinae
(Fig. 7-4)

Literature.--Brunner von Wattenwyl (1895); Kirby (1906); Bruner (1915); Hebard (1927), Sjöstedt (1933); Zeuner (1936); Beier (1954, 1962); Robinson 1969b; Belwood (this study, Chap. 6).

Description.--Medium-large, slender, long winged and cylindrical. Wings taper to a point apically. Overall coloration light and lichenose, with varying amounts of light greys, brown, beiges, and greens. Hind wings alternating blackish and whitish squares. Frons darker than rest of head, palps cream. Abdominal sternites reddish. Oviposi-

tor long, straight, stiff, and bladelike, with distal half serrated and darker than proximal half.

Specimens Examined.--3 females, 8 males, including 83-48, 83-140, 83-166, 83-233, 83-283, 83-288, 83-322, 83-324, 84-73, 84-231, 84-288.

Measurements.--TL: females 79.9 (± 3.0), males 67.9 (± 2.5). BL: females 49.8 (± 2.3), males 43.5 (± 1.9). LLFW: females 65.1 (± 3.3), males 53.7 (± 2.3). WLFW: females 11.1 (± 0.6), males 8.5 (± 0.4). ANT: females 112.3 (± 3.3), males 125.2 (± 15.1). OVIP: 34.1 (± 1.0). Weight: females 4.9 (± 0.9), males 2.9 (± 0.2).

Months Collected (as adults).--January, February, March, April, May, June, July, September, October, November.

Relative Abundance.--Uncommon.

Habitat.--Mostly in forest understory.

Diet in Lab.--Herbivorous.

Predators on BCI.--A few remains found in roost of bat believed to be Tonatia silvicola (Belwood, unpublished data). Call of this insect was used to attract T. silvicola in laboratory studies (Belwood this study, Chap. 6).

Defensive Behaviors.--Sit on lichen covered surfaces, often with body concealed in depressions or cavities on wood. When disturbed, adopt a characteristic posture in which the fore and hind wings are raised and exposed vertically. This also exposes the reddish belly (see Robinson 1969b for full description). When handled, males

produce a disturbance stridulation and sometimes flail their legs. Males stop singing when disturbed.

Dayroost in Cage.--On logs and twigs, preferably lichen covered, as described above.

Dayroost in Field.--Presumably as above.

Location at Night.--Seen on tree trunks. Occasionally attracted to lights.

When Active at Night.--Mid to late evening (2000 to 0200 h).

Other Observations.--Females lay eggs in wood.

Signal Analysis.--The airborne call was heard as a single loud zip, which was followed by a long period of silence before the zip was repeated (Fig. 7-4a,b). Slowed, the call consisted of four pulses (Fig. 7-4c), the first of which was low and constant in amplitude (a refrain). This is followed by three pulses each of which increase progressively in length and amplitude. The final pulse is the longest and highest in amplitude and it decays rapidly.

At 25°C, 4.4 ± 2.2 such calls were produced per 5 min period ($n = 68$) in 6 animals. Calls lasted 0.11 ± 0.02 s ($n = 13$). The low and high frequencies of the call were 5400 and 49,800 kHz, respectively. Peak frequencies in the calls of 2 animals were 13.0 and 16.8 kHz, respectively. Call intensity in one animal was 115 dB at 5 cm. The duty cycle of the airborne call was 0.16.

Substrateborne calls were observed in males and females. In males, they consisted of a long continuous train of 25.9 ± 7.6 bounces ($n = 15$). In 5 males, $1.2 (\pm 1.8)$ tremulation bouts were produced per 5 min period ($n = 24$). The tremulations were 1.09 ± 0.4 s long ($n = 15$) for a duty cycle of 0.44.

Males in the laboratory called between 2030 and 0200 h, and continued to call in a large flight cage, in the presence of flying bats (*Tonatia silvicola*) that were attracted to their calls (Belwood this study, Chap. 6). These katydids occasionally moved about their cages and groomed between calling bouts, but not while they actually called. They called in several positions (e.g., head up or head down). Combined duty cycle of the advertisement call was 0.6, of which 26.7% was airborne and 73.3% was substrateborne.

Balboa tibialis (Brunner von Wattenwyl)
Pseudophyllinae
(Fig. 7-5)

Literature.--Brunner von Wattenwyl (1895); Saussure and Pictet (1898); Hebard (1927, 1933); Beier (1954, 1962).

Description.--Large-medium, heavy bodied, long winged and cylindrical. Overall coloration varies from light to dark to greenish brown. Pronotum usually greyish taupe with large semi-circular posterior disc. Tegmina usually lighter

except for long blackish brown patches that extend from the anterior to middle portion of each tegmen. Legs grey-brown with irregular lighter patches. Eyes and long thin antennae brown; eyes blend in with face. Cells of hind wings dark brown, veins cream. Ovipositor rigid, straight and blade-like, with serrations on distal half of dorsal margin; proximal half cream, distal half dark brown. Cerci bright green or brown.

Specimens Examined.--1 female, 7 males, including 83-38, 83-55, 83-274, 83-276, 83-282, 83-347, 84-42, 84-86.

Measurements.--TL: female 59.3, males 51.8 (± 2.2). BL: female 46.4, males 44.0 (± 2.8). LLFW: female 48.8, males 40.1 (± 1.8). WLFW: female 11.1, males 10.2 (± 0.5). ANT: female 140, males 130.0 (± 9.2). OVIP: 21.9. WT: males 4.8 (± 0.7).

Months Collected (as adults).--March, April, May, June, August, October, November.

Relative Abundance.--Uncommon.

Habitat.--Usually in forest understory; sometimes in forest edge.

Diet in Lab.--Herbivorous.

Known Predators on BCI.--Rarely taken by foliage glean-ing bats (Belwood this study, Chap. 4). Constituted about 2% (by weight) of the diet of Micronycteris hirsuta on BCI over a two year period.

Defensive Behaviors.--Dayroost in concealed areas.

Dayroost in Cage.--Crevices in wood or bark; sometimes on the ground in leaf litter.

Dayroost in Field.--Not known, but presumably as above.

Location at Night.--On woody plant matter; occasionally at lights.

When Active at Night.--Mid to late evening (2100 to 0400 h).

Other Observations.--Females oviposit in wood. In the laboratory, one female was observed as she laid 22 eggs in a live tree branch with a girth of about 10 cm. Another female took 4 h to lay 122 eggs in a hard slab of wood. The eggs were placed deep in the wood next to one another, with only a small tail-like projection visible for each. Within a few minutes, ants were attracted to the area where the eggs had been laid.

The spermatophore is four lobed and on one female mated in captivity, measured about 15 by 13.5 mm, and weighed 1.05 g. This represented 21.9% of the body weight of the male that produced it.

Signal Analysis.--The airborne call was heard as a single raspy zip (Fig. 7-5a,b). Slowed, it consisted of two pulse trains (Fig. 7-5c), the first of which contained about seven short pulses of equal amplitude. Each of these pulses increased rapidly in amplitude and decayed quickly (Fig. 7-5d). The second pulse train, which followed a short silent

period, consisted of three or four pulses, which decreased in amplitude sequentially.

A total of 21.2 ± 12.0 such calls were produced per 5 min period ($n = 82$) in 7 animals. Calls lasted 0.2 ± 0.03 s ($n = 34$). The low and high frequencies of the calls of two animals are 6.6 and 7.7, and 17.6 and 17.7 kHz, respectively. Peak frequencies in the calls of these two males were 12.9 and 13.1 kHz, respectively. Call intensity was not measured. The duty cycle of the airborne call is 1.41.

Substrateborne calls were observed and recorded in males and females. In each sex, tremulation consisted of a long train of bounces that were produced in quick succession. In males (Fig. 7-5e), the mean number of bounces was 31.9 ± 5.9 per train ($n = 37$) without a female present. Each bout lasted 4.8 ± 0.9 s ($n = 34$). Female tremulation bouts were similar to those of males (Fig. 7-5f). They consisted of 35.2 ± 5.9 individual bounces and lasted 5.0 ± 0.7 s ($n = 6$). In 2 males, 1.9 (± 2.2) tremulation bouts were produced per 5 min period ($n = 24$), with no female present. When a female was present and responded to the male with tremulations of her own, tremulation bout production increased to 12.3 ± 3.1 per 5 min period ($n = 24$). In males, one tremulation bout was usually performed after a longer series of acoustic calls. One individual's acoustic call (A) and tremulation call (T) patterns for four 5 min periods are given below [an asterisk (*) denotes that

the airborne and substrateborne signals were produced together]:

- 1) T Ax9 T Ax11 T Ax9 T Ax14.
- 2) 5xA T 20xA T 20xA T A
- 3) Ax16 T*A Ax21 T Ax9 T*A Ax7 T*A A A T A A T*A A
- 4) A T Ax3 T*A T A A T*A T*A T T Ax8 T Ax10 T Ax8 T*A Ax9

The duty cycle of the tremulation call was 3.04. That of both call types combined was 4.45, 31.7% of which was the airborne call and 68.3% of which was the tremulation signal.

Males in the laboratory called between 2100 and 0330 h. These animals remained perfectly still for hours at a time while they produced their acoustic calls. They called from both horizontal and vertical surfaces. These insects are fairly heavy bodied and the abdomen is large. In both males and females the abdomen often made contact with the substrate during tremulation.

Cocconotus wheeleri Hebard
Pseudophyllinae
(Fig. 7-6)

Literature.--Hebard (1927); Beier (1960); Belwood this study (Chap. 4). Morris and Beier (1982) describe the airborne calling song of C. pusillus.

Description.--Medium, slender, cylindrical and long winged. Sides of pronotum, abdomen, and legs light taupe.

Face cream with five vertical and sharply defined blackish brown stripes. Eyes teal blue and antennae at least twice body length and dark brown. Occiput and vertex suffused with blackish brown. Dorsal portion and anterior and posterior margins of pronotum blackish brown. The numerous veins on the tegmina cream except for those along proximal third of costal margin, which are greenish yellow. Ovipositor sharp, bladelike and curved upwards toward dorsum; margins dark brown, center cream with serrations on distal half of dorsal and ventral margins.

Specimens Examined.--9 females, 5 males, including 83-195, 83-214, 83-216, 83-231, 83-241, 83-246, 83-248, 83-285, 83-293, 84-104, 84-320, 84-343.

Measurements.--TL: females 53.5 (± 3.4), males 42.7 (± 1.3). BL: females 38.4 (± 3.6), males 37.1 (± 1.7). LLFW: females 38.7 (± 1.6), males 33.9 (± 0.8). WLFW: females 7.8 (± 0.4), males 7.0 (± 0.1). ANT: females 103.8 (± 14.2), males 103.2 (± 12.4). OVIP: 18.6 (± 0.8). WT: females 2.3 (± 0.4), males 1.7 (± 0.7).

Months Collected (as adults).--February, March, April, May, July, August, September, October.

Relative Abundance.--Common.

Habitat.--Most common in forest understory; also at forest edge.

Diet.--Herbivorous in lab. Seen eating small white mushrooms on rotten log in the field.

Predators on BCI.--Foliage gleaning bats, particularly Micronycteris hirsuta (Phyllostomidae: Phyllostominae) (Belwood this study, Chap. 4), where they constitute about 23% of the diet by both number and biomass; probably also diurnal forest-dwelling birds that forage for insects in or on leaves (Greenberg and Gradwohl 1980; Gradwohl and Greenberg 1982, 1984).

Defensive Behaviors.--Dayroost in concealed places. Stop singing when disturbed.

Dayroost in Cage.--Mainly in curled leaves; sometimes in cracks and crevices on slabs of wood. One individual returned to the same curled dead leaf in its cage on eight consecutive days.

Dayroost in Field.--Found in unfurled Heliconia leaves (height 75 cm) and in nearby PVC stakes (30 cm high, 2.5 cm diameter) used as markers in the forest; presumably also as above.

Location at Night.--On broad leaves or twigs of herbaceous plants or small trees; occasionally at lights.

When Active at Night.--Early to mid evening (1900 to 2400 h).

Other Observations.--One female in the field was observed ovipositing in a rotten log on the ground. Captive females often oviposit in the wooden frames of their cages. Inside curled dead leaves, the five facial stripes help camouflage the insect's face.

Signal Analysis.--The airborne call is heard as a faint, but noisy zip that is produced at regular intervals (Fig. 7-6a,b). Slowed, each zip consists of 12 to 16 major pulses, each of which is followed by relatively low amplitude minor pulse (Fig. 7-6c). Each major pulse is short, rises moderately fast in amplitude, then falls abruptly once maximum amplitude is achieved (Fig. 7-6d). At 26°C, 6.5 ± 5.7 zips were produced per 5 min period ($n = 39$) in 4 animals. Zips lasted 0.4 ± 0.04 s ($n = 20$). The low and high frequencies of the zip were 15.6 and 41.6 kHz, respectively. Peak frequencies in the calls of 2 animals were 26.0 kHz. Call intensity in one animal was 97 dB at 10 cm. The duty cycle of the airborne call was 0.87.

3.5 ± 5.2 ($n = 36$) substrateborne calling bouts per 5 min period ($n = 36$) were observed in three males and each lasted a total of 0.2 ± 0.1 s ($n = 41$). This represents a duty cycle of 0.23. Each bout consisted of a bounce train of 1 to 4 bounces. The mean number of bounces per bounce train was 2.1 ± 0.6 ($n = 44$), and each bounce lasted 0.07 ± 0.01 s (check with original tape). The interval between bounces was 0.05 ± 0.01 s. Tremulation was also observed in females, but was not examined in detail. The combined duty cycle of the sexual advertisement calls was 1.1, of which 79.1% was the airborne signal and 20.9% the substrateborne.

Males in the laboratory were observed to call between 2000 and 2400 h. These animals moved about their cages

incessantly between the production of airborne and sub-strateborne calls and sometimes also while calling. Calling continued in the presence of short bursts of ultrasound (40 and 80 kHz, respectively) that were intended to mimic bat echolocation calls.

Comparison with Calls of Congeneric.--Morris and Beier (1982) describe the airborne calls of C. pusillus n. sp. from the Costa Rican uplands (Monteverde). The song parameter values that follow below in parentheses are for this insect and C. wheeleri, respectively.

C. pusillus is considerably smaller than C. wheeleri (male TL: "about 2 cm"; 42.7); both species are relatively abundant, and have long antennae and black facial markings. Both species also produce short airborne calls, although those of C. pusillus are produced more often (0.2 per s; 0.02 per s). The calls of C. pusillus have a lower peak frequency than those of the other insect (10 kHz vs 26 kHz).

Copiphora brevirostris Author
Copiphorinae
(Fig. 7-7)

Literature.--Hebard (1927); Belwood this study (Chap. 65). See also species account for C. nr brevirostris (this chapter). Morris (1980) describes the calling and tremulation behavior of the closely related C. rhinoceros.

Description.--Large-medium, long, slender, long winged, lime green katydid, although bright orange morphs also occur. Eyes, frons, mandibles, clypeus, and labrum straw colored. Mandibles large. Distal third of costal wing margin and all of the apical, lateral and anal margins pinkish. Tegmina sparsely dotted with small blackish flecks. Ovipositor green, very long (longer than body), thin, flexible, and uniform in width.

Specimens Examined.--9 males, 10 females, including 82-2, 82-14, 82-51, 83-164, 83-224, 83-226, 83-227, 83-266, 83-284, 83-286, 83-340, 84-35, 84-74, 84-160, 84-254, 84-259, 84-272, 84-279, 84-356.

Measurements.--TL: males 62.0 (± 2.0), females 125.6 (± 4.7). BL: males 42.8 (± 2.8), females 44.4 (± 2.9). LLFW: males 52.2 (± 1.7), females 57.6 (± 1.9). WLFW: males 11.0 (± 0.4), females 11.9 (± 0.6). ANT: males 83.6 (± 8.9), females 87.6 (± 2.7). OVIP: 86.6 (± 4.0). WT: males 2.5, females 2.9 (± 0.5).

Months Collected (as adults).--January, February, March, May, June, July, August, September, October, November.

Relative Abundance.--One of the most common katydids on BCI.

Habitat.--Forest understory.

Diet.--Ate live insects in captivity, about one small (10 to 15 mm BL) insect (moth, fly, cicada, other katydid)

every two or three days. Would not eat small (< 10 mm BL) scarab beetles. One field collected specimen had insect remains in its gut, and several others at different times of the year had bright orange plant material in their crops.

Known Predators on BCI.--Although abundant on BCI, constitute only about 2% by weight of the diet of the bat Micronycteris hirsuta (Belwood this study, Chap. 4); also taken by nocturnal wolf spiders (Belwood, personal observation), and some diurnal forest-dwelling birds (see Hebard 1927:139; Greenberg and Gradwohl 1980; Gradwohl and Greenberg 1982, 1984).

Defensive Behaviors.--Inflict painful bite with large mandibles and will regurgitate crop contents when handled. Stop singing when disturbed.

Dayroost in Cage.--Under surfaces of green leaves.

Dayroost in Field.--Observed in curled Heliconia leaves, 0.5 to 1.0 m off the ground, and on under surfaces of green leaves.

Location at Night.--On upper surfaces of broad leaves, and on woody stems of plants, 0 to 400 cm above ground. Sometimes at lights.

When Active at Night.--Mid to late evening--about 2200 to 0400 h.

Other Observations.--Two pairs were observed mating in the laboratory and remained in copula for 55 min and 30 min, respectively. In one pair, the spermatophore given to

the female represented 12.8% of the male's body weight. In the lab, a female was observed laying eggs at the base of a plant; about 5 cm of her ovipositor was inserted into the soil. At night in the field, females are often seen on the ground walking through leaf litter. The tan face camouflages the insect inside the curled green leaves that constitute its diurnal roost.

Signal Analysis.--The airborne call was heard as a short, single, noisy but high-pitched zip (Fig. 7-7a,b). Slowed, each zip consists of five closely spaced major pulses, each of which rises quickly in amplitude and is higher in amplitude than the pulse preceeding it. Minor pulses follow each major pulse.

At 24.5°C, 1.9 (± 1.9) zips were produced per 5 min period (n = 78) in six animals. Calls lasted 0.09 (± 0.01) s. The low and high frequencies of the call were 8.8 and 48.2 kHz, respectively. Peak frequencies in the calls of 4 animals were 14.0, 15.2, 15.6, and 15.8 kHz (Peak 1) and the harmonically related 30.6, 31.4, 31.6 and 32.0 kHz (Peak 2), respectively. The second peaks were the most intense. Call intensity in 2 animals was 95 dB at 30 cm, and 100 dB at 16 cm, respectively. The duty cycle of the airborne call was 0.06, the lowest of all the forest katydids examined on BCI.

Substrateborne calls were observed in both males and females, and were the most complex of all the species studied. In males each tremulation bout consisted of about four

(3.5 ± 0.8 , $n = 26$) bounce train groups, that together lasted a total of 2.23 ± 0.5 s ($n = 16$). Individual bounce train groups lasted 0.3 ± 0.1 s ($n = 40$) and were 0.4 ± 0.1 s apart ($n = 64$). In males, $7.7 (\pm 3.7)$ tremulation bouts were produced per 5 min period ($n = 59$). Tremulation duty cycle was 5.72. Combined airborne and substrate borne duty cycle was 5.78, of which 1% was the airborne call and 99% was the substrateborne call.

Males in the laboratory called between 0100 and 0430 h. They were stationary during the production of all calling signals, although they often ate (i.e., chewed) and called simultaneously. Occasionally they moved a few cm between calling bouts. When males called on vertical surfaces their heads were usually oriented toward the sky. Females responded to male tremulations with tremulations of their own. These resembled those of males but were longer. They were not recorded.

Comparison with Calls of Congenerics.--The airborne calls of C. brevirostris and C. nr brevirostris (this chapter) are almost identical in terms of frequency spectra, and audiospectrograms and oscillograms of individual call notes. The major differences in calling behavior concern note (zip) repetition rates. There is one note per call in C. brevirostris while there are several notes per call in C. nr brevirostris. Differences in temporal rather than spectral aspects of the call are known to distinguish the

songs of other sympatric congeners [e.g., Homorocorhyphus spp. Bailey and Robinson (1971)].

The airborne call of C. brevirostris, however, is very different from that of C. rhinoceros Pictet from lowland Costa Rica (Morris 1980), even though members of both species are the same size and occur in similar habitats (Belwood, personal observation). (C. rhinoceros also occurs on BCI, but is extremely rare. Only one individual, a female not considered here, was found as part of this study.) The values given below in parentheses are for C. rhinoceros and C. brevirostris, respectively.

The calls of C. rhinoceros are lower in pitch than those of C. brevirostris [carrier frequency 8.7 kHz with less intense harmonics at 17 and 26.1 kHz (Morris 1980:Fig. 3A); suppressed first harmonic at about 15 kHz and major peak at 31 kHz (Fig. 7-7a)]. C. rhinoceros also produced calls more frequently (40 to 50 per min; 0.4 per min).

Oscillographic tracings of the calls are also different. Those of C. rhinoceros consist of a minor pulse train lasting about 14 ms that consists of about 7 low amplitude rapid decay pulses. This is followed by a simple prolonged major pulse of higher amplitude that lasts about twice as long (Morris 1980:Fig. 3B). C. brevirostris' calls on the other hand, are at least five times longer than the other species' (0.5 to 1.0 s; 90 ms), and their structure is similar only to the other's first (minor) pulse train.

The sexual advertisement signals of both C. rhinoceros and C. brevirostris incorporate airborne and substrateborne signals, which are produced in alternating fashion. Also, the tremulations are similar in structure. Members of both species produce several tremulations per bout (means: 3.1; 3.5), and bout lengths are similar (means: 2.4 s; 2.23 s). In both cases, these were produced in the absence of conspecifics and females produced signals that were similar to those of the males, but shorter.

Copiphora nr brevirostris
 Copiphorinae
 (Fig. 7-8)

Literature.--see account for C. brevirostris.

Description.--As C. brevirostris above, but frons and genae shiny brownish black, labrum cream, and eyes bright pink. Slightly smaller than C. brevirostris, and ovipositor about two-thirds length of that of the above. Some specimens have two small black dots on the posterior quarter of the pronotum.

Specimens Examined.-- 8 females, 3 males, including 83-162, 83-323, 83-294, 84-317, 84-329, 84-337, 84-338, 84-355, 84-362, 84-363, 84-366.

Measurements.--TL: females 98.8 (\pm 4.8), males 56.7 (\pm 1.8). BL: females 42.6 (\pm 3.6), males 37.0 (\pm 1.8). LLFW: females 49.5 (\pm 1.6), males 43.6 (\pm 0.2). WLFW: females

11.1 (± 0.7), males 9.6 (± 0.4). ANT: females 105 (± 2.5), males 75 (all broken). OVIP: 62.1 (± 1.9). WT: females 2.6, males 1.5.

Months Collected (as adults).--August, September, October, November, December.

Relative Abundance.--Uncommon.

Habitat.--Seen only in forest understory.

Diet.--Herbivorous and probably carnivorous like Copiphora brevirostris, which it resembles closely.

Predators on BCI.--Unknown, but presumably as for C. brevirostris.

Defensive Behaviors.--Inflict painful bite when handled.

Dayroost in Cage.--Not known; presumably as for C. brevirostris.

Dayroost in Field.--Not known; presumably as for C. brevirostris.

Location at Night.--One seen walking on cleared trail in forest; several others seen on broadleaf vegetation, about one m off ground.

When Active at Night.--Very late evening (0200 to 0500 h).

Other Observations.--None.

Signal Analysis.--Only seven and nine airborne calls, respectively, were produced by two animals on successive evenings. The call is a series (bout) of short, loud, raspy

zips produced in quick succession (Figs. 7-8a,b,c). Each call contained 3.8 ± 4.0 individual zips ($n = 16$ calling bouts), each of which lasted 0.3 ± 0.1 s ($n = 33$). Slowed, each zip consists of five alternating minor and major pulses, each of which increase gradually in amplitude, then drop off sharply (Fig. 7-8d). Pulse trains were separated by intervals of 0.5 ± 0.1 s ($n = 28$). The interval between calling bouts was 4.1 ± 1.8 min ($n = 14$). The low and high frequencies of the call were 8.4 and 38.6 kHz, respectively. Peak frequencies in the calls of the two animals were 14.2 and 28.5, and 14.6 and 29.0, respectively, and were harmonically related. Calls were intense; in two animals they were recorded as 110 dB at 20 cm, and 84 dB at 3 m, respectively.

Substrateborne calls were not studied in this species.

Males in the laboratory were called only very late in the evening, between 0300 and 0400 h. They were very still while they called.

Comparison with Calls of Congenerics.--See species account for C. brevirostris.

Docidocercus gigliotosi (Griffini)
Pseudophyllinae
(Fig. 7-9)

Literature.--Griffini (1896a); Saussure and Pictet (1898); Hebard (1927, 1933); Beier (1962); Belwood this

study (Chap. 4); song description for D. chlorops n. sp. in Morris, Klimas and Nickle (in press).

Description.--Medium, slender, cylindrical, long winged katydid. Tegmina rusty taupe brown, but papery and slightly translucent; apical margin slightly truncated. Posterior portion of genae, abdominal sternites, cerci and claspers cream. Basal quarter of legs rusty brown. Base of antennae, frons and anterior margins of genae turquoise blue. Median ocellus whitish cream. In some specimens there is a lime green or yellow hour glass shaped spot on dorsal surface of prothorax. Costal margins on front wings also sometimes yellowish. Distal margin of abdominal tergites bordered in dark brown. Ovipositor rigid, sharp and bladelike, with slight serrations on dorsal margin; proximal half cream, distal half dark brown.

Specimens Examined.-- 13 females, 10 males, including 82-24, 83-87, 83-168, 83-169, 83-218, 83-263, 83-264, 83-265, 83-299, 83-300, 83-307, 83-335, 83-351, 84-244, 84-245, 84-250, 84-280, 84-315, 84-319, 84-323, 84-324, 84-326.

Measurements.--TL: females 49.9 (\pm 2.0), males 45.6 (\pm 1.5). BL: females 37.9 (\pm 4.0), males 36.4 (\pm 2.2). LLFW: females 40.5 (\pm 1.8), males 37.3 (\pm 1.0). WLFW: females 8.1 (\pm 0.5), males 7.3 (\pm 0.2). ANT: females 155, males 136. OVIP: 17.1 (\pm 0.5). WT: females 1.8 (\pm 0.3), males 1.6 (\pm 0.2).

Months Collected (as adults).--April, May, June, July, August, September, October, November, December.

Relative Abundance.--Abundant; one of the most abundant katydid species on BCI.

Habitat.--Forest understory; sometimes forest edge.

Diet in Lab.--Herbivorous.

Predators on BCI.--Constitute 19.1% by number, and 16.4% (by weight) of the diet of the foliage gleaning bat Micronycteris megalotis (Belwood this study, Chap. 4); probably also preyed on by diurnal birds that forage in aerial leaf litter (sensu Gradwohl and Greenberg 1982, 1984).

Anti-predator Behaviors.--Dayroost in aerial leaf litter; stop singing when disturbed.

Dayroost in Cage.--Curled dead leaves, cracks and crevices on logs. Return to same dead leaves day after day.

Dayroost in Field.--Curled dead leaves that hang from trees. Also in curled Heliconia leaves. This occurs in adults and nymphs of all sizes. Anecdotal evidence suggests that adults return to the same roosts day after day.

Location at Night.--On leaves and stems of shrubs and small trees 40 to 150 cm off ground.

When Active at Night.--Early evening (1830 to 2400 h).

Other Observations.--Mating was observed in one captive pair in which individuals remained in copula for 2 min 8 s. The male produced a three-lobed spermatophore that

constituted 15.4% of his body weight. Females oviposit in wood. The blue face color camouflages the insects face inside dead leaves.

Signal Analysis.--The airborne call of D. gigliotosi was heard as one, or usually two, faint, high-pitched and pure toned ticks (Fig. 7-9a,b). Slowed, each tick was one prolonged pulse whose onset was gradual. At 26°C, 21.6 ± 10.9 such calls were produced per 5 min period ($n = 66$) in 7 animals. Single pulses lasted 0.034 ± 0.01 s ($n = 46$), and were produced singly or in groups of two or three. The production of 638 pulses was observed. Of these 339 (53.1%) were one pulse calls, 296 (46.4 %) were two pulse calls, and 3 (0.5%) were three pulse calls. The interval between pulses that were produced together was 0.182 ± 0.02 s ($n = 50$). The low and high frequencies of the call are 19.0 and 27.6 kHz, respectively. The peak frequencies in the calls of 3 animals was 22.4 kHz. Call intensity in these animals was 94 dB at 10 cm, 105 dB at 3 cm, and 103 dB at 7 cm, respectively. The duty cycle of the airborne calling song is 0.35.

Substrateborne calls were observed in males and also in females that responded to males. In males the tremulation bout consisted of a short bounce train consisting of 9.5 ± 2.8 bounces ($n = 10$) (Fig. 7-9d). Each lasted 0.77 ± 0.2 s ($n = 10$). In 7 males 16.4 ± 12.2 tremulation bouts were

produced per 5 min period ($n = 38$). The duty cycle of the substrate borne calls was 4.21.

Males in the laboratory called between 1730 and 2300 h. These animals often moved about their cages between the production of both airborne and substrateborne calls, which were produced in seemingly random alternating fashion. Occasionally, both types of calls were produced simultaneously. Airborne (A) and tremulation (T) call production patterns for three 5 min intervals for one individual are given below [an asterix (*) between T's and A's indicate that these calls were produced at the same time; one between A's indicates that two airborne calls were produced in immediate succession]:

1) T A*A T A T T*A T*A T A*A A

2) A T A T A T A*A T A*A T T T A*A T T A*T A*T T A*A T
A T A A*A T A T

3) T A*A T T A*A T A A T A*A A T A*A T A T A T T A*A T
A T*A*A T

The combined duty cycle of the advertisement calls was 4.56, of which 7.7% was airborne and 92.3% was substrateborne calls.

Comparison with Calls of Congeneric.--Morris, Klimas and Nickle (in press) describe the call of D. chlorops n. sp. from Rio Palenque, Ecuador. This insect and its Panamanian counterpart share several notable features. (The

values that follow in parentheses are for D. chlorops and D. gigliotosi, respectively.)

These insects are approximately the same size (male TL: 45.8; 45.6), both occur in lowland tropical forests and both have blue-green faces. Both species tremulate and produce an airborne call with ultrasonic carrier frequencies (24 kHz; 22.4 kHz). Call repetition rates are also similar (1 per 21.1 s; 1 per 13.8 s), and the duty cycles are extremely low (0.3; 0.35). However, some differences occur between the signals. The call of D. gigliotosi (182 ms) is about three times the length of that of D. chlorops (63 ms). The latter's call also has second and third harmonics (at 48 and 72 kHz) and is frequency modulated. This does not occur in the other's call.

Eucocconotus camerani (Griffini)
Pseudophyllinae
(Fig. 7-10)

Literature.--Griffini (1896a); Saussure and Pictet (1898); Giglio-Tos (1898).

Description.--Large, long-winged, cylindrical katydid. Vertex dark brown, genae camel colored with two black facial stripes extending from base of the middle of each eye toward mandible. Frons black. Eyes dark cream with brown-turquoise green tint. Antennae at least twice body length. Pronotum dark brown, almost black, with numerous small scattered protuberances. Veins on wings cream with blackish

taupe cells between veins giving the wings a mottled appearance. Abdomen cream. Legs dark cream with brown-turquoise tint. Ovipositor long, flexible and rigid, but not bladellike; distal three-quarters brown, proximal quarter cream; lacks serrations.

Specimens Examined.--3 females, 1 male, including 84-187, 84-221, 84-334.

Measurements.--TL: females 67.1 (± 3.2), male 67.2. BL: females 46.6 (± 4.2), male 53.5. LLFW: females 56.7 (± 2.5), male 57.5. WLFW: females 12.0 (± 0.3), male 11.8. ANT: female 140, male 142. OVIP: 29.8 (± 0.8).

Months Collected (as adults).--May, August.

Relative Abundance.--Uncommon.

Habitat.--Seen only in forest understory.

Diet in Lab.--Herbivorous.

Predators on BCI.--Not known, but probably forest-dwelling birds that forage during the day for insects in or on leaves (Greenberg and Gradwohl 1980; Gradwohl and Greenberg 1982, 1984).

Defensive Behaviors.--Dayroost in concealed places.

Dayroost in Cage.--In curled leaves.

Dayroost in Field.--Found 12 last instar nymphs in white PVC pipe stakes (30 cm high, 2.5 cm diameter) used to make the seed traps commonly used in various botanical studies on BCI. Presumably also dayroost in other pipelike

structures in forest vegetation (e.g., curled Heliconia leaves).

Location at Night.--One male found on a tree trunk, 2 m high at approximately 2000 h. This animal was heard calling, and is the only forest katydid collected as part of this study that was found in the field by its call.

When Active at Night.--Early evening (2000 to 2200 h).

Other Observations.--Black facial stripes camouflage the insect's face when it roosts in leaves.

Signal Analysis.--The airborne calls are short, harsh, loud, and raspy, sporadically produced zips (Fig. 7-10a,b). Slowed, each zip consists of two (sometimes three) major pulse train groups, each of which is preceeded by a constant amplitude refrain (Fig. 7-10c). Each PTG consists of 13-20 short, relatively rapid onset, rapid decay pulses. Within a PTG, the tendency is for an overall increase in amplitude. At 25.5°C, 1.4 ± 0.5 zips were produced per 5 min period ($n = 9$) in one animal. Zips lasted 0.17 ± 0.03 s ($n = 6$). The low and high frequencies of the call are 13.1 and 36.3 kHz, respectively. Peak frequencies in the calls of 2 animals were 23.4 and 22 kHz, respectively. Call intensity in one animal was 111 dB at 18 cm. The duty cycle of the airborne call is 0.08.

Substrateborne calls were observed and recorded in males only, although they were also seen in females who responded to males. In males, tremulation production was

observed only in individuals that were in the presence of females (i.e., lone males were not observed). In 3 males, 102 ± 40.0 tremulations were produced per 5 min period ($n = 15$) under these conditions. They were long and forceful and consisted of a train of about 10.1 ± 1.3 bounces ($n = 24$). Each complete bout lasted 1.6 ± 0.2 s.

Males in the laboratory were heard to call between 2000 and 2100, but calling probably also occurs at other times.

Idiarthron major Hebard
Pseudophyllinae
(Fig. 7-11)

Literature.--Hebard (1927); Beier (1960); Belwood this study (Chap. 4).

Description.--Large-medium, cylindrical moderately robust, long winged katydid. Antennae at least twice body length. Eyes, face, antennae, body and tegmina medium cinnamon brown. The larger scattered cells formed by numerous veins on tegmina dark reddish-blackish brown. Conjunctival membrane between abdominal sternites grey. Ovipositor straight, rigid and bladelike with pronounced serrations on the distal half of the dorsal margin; proximal third cream, distal two-thirds very dark brown, almost black. In some specimens, the joints between each femur and tibia are cream, as is the dorsal surface of the pronotum.

Specimens Examined.--4 females, 4 males, including 83-344, 84-132, 84-154, 84-177, 84-335.

Measurements.--TL: females 59.6 (\pm 3.5), males 49.9 (\pm 0.8). BL: females 42.5 (\pm 4.2), males 42.7 (\pm 1.3). LLFW: females 40.2 (\pm 1.3), males 38.4 (\pm 2.1). WLFW: females 10.2 (\pm 0.3), males 8.9 (\pm 0.7). ANT: females 112.7 (\pm 11.5), males 110.1 (\pm 14.0). OVIP: 21.2 (\pm 0.3). WT: females 3.6 (\pm 0.8), males 2.7 (\pm 0.2).

Months Collected (as adults).--February, March, May, June, July, September, October, November.

Relative Abundance.--Uncommon.

Habitat.--Mainly in forest understory.

Diet in Lab.--Herbivorous.

Predators on BCI.--Constitute about 7% (by number) and 12% (by weight) of the diet of the foliage gleaning bat Micronycteris hirsuta over a two year period on BCI (Belwood this study, Chap. 4).

Defensive Behaviors.--Dayroost in concealed locations. Stop singing when disturbed.

Dayroost in Cage.--Mainly in crevices on woody substrates, less often in leaf curls and leaf litter.

Dayroost in Field.--Not observed, but presumably as above.

Location at Night.--Seen on woody shrubs and trees. Sometimes at lights.

When Active at Night.--Early to mid evening (2100 to 2400 h).

Other Observations.--None.

Signal Analysis.--The airborne call is heard as a single loud zip (Figs. 7-11a,b). Slowed, each zip consists of two distinctive pulse trains (Fig. 7-11c). The first, a refrain, consists of about 11 low amplitude pulses in quick succession. Pulses in the second pulse train are higher in overall amplitude. In the second pulse train, there are 10-13 major pulses. The first five or so increase gradually in amplitude and length and are followed by four to six pulses at maximum amplitude, which increase successively in length. The last two pulses are relatively short and decrease in amplitude. At 27°C, 2.10 (\pm 2.38) calls were produced per 5 min period (n = 84) in 5 animals. Calls lasted 0.10 (\pm 0.03) s (n = 20). The low and high frequencies of the calls were 15.8 and 33.0 kHz, respectively. Peak frequencies in the calls of 2 animals were 23.0 and 27.2 kHz, respectively. Call intensities at 10 cm in 3 animals were 104, 100, and 95 dB. The duty cycle of the airborne call is 0.07.

Substrateborne calls were observed only in males, and were not tape recorded. In 5 animals, 3.0 (\pm 2.1) tremulation bouts were produced per 5 min period (n = 48). These were only produced when the insects were on woody surfaces.

Males in the laboratory called between 2100 and 2400 h, and walked slowly about their cages between, but not during, calling bouts. They remained perfectly still while they called.

Ischnomela pulchripennis Rehn
Pseudophyllinae
(Fig. 7-12)

Literature.--Rehn (1906), (Hebard 1933), Beier (1960), Belwood this study (Chap 6).

Description.--Large-medium, long winged, cylindrical katydid. Antennae at least twice body length. Eyes, pronotum, and most of tegmina and hind femora turquoise blue. Most of head, antennae, prothoracic tibiae and mesothoracic legs camel brown. Ventral surface of all legs with a dark brown border and veins near costal wing margin, especially near humeral angle, cream. Long, thin, slightly fleshy cream ovipositor with slight upward curve; lacks serrations.

Specimens Examined.--2 females, 4 males, including 82-42, 83-33, 84-313, 84-354, 84-367, 84-368.

Measurements.--TL: females 61.1 (± 0.7), males 57.0 (± 0.3). BL: females 44.3 (± 4.3), males 50.2 (± 1.8). LLFW: females 49.6 (± 0.3), males 45.8 (± 0.7). WLFW: females 10.6 (± 0.3), males 9.2 (± 0.3). ANT (most broken): males 93.0. OVIP: 20.4. WT: males 4.4 (± 0.1).

Months Collected (as adults).--February, March, May, June, July, October, November.

Relative Abundance.--Uncommon.

Habitat.--Forest understory, often associated with the large terrestrial bromeliad Aechmea magdalenae; sometimes in vegetation at forest edge.

Diet in Lab.--Herbivorous.

Predators on BCI.--Not known. Calling males attracted foliage gleaning bats during a field study on BCI (Belwood this study, Chap. 6), but did not appear to be taken as food by the two species for which detailed feeding habits are known (Belwood this study, Chap. 4).

Defensive Behaviors.--Associated with A. magdalenae, a terrestrial bromeliad with long sharp spines. Has low disturbance threshold with respect to song cessation.

Dayroost in Cage.--In curled leaves.

Dayroost in Field.--Not known, but presumably as above.

Location at Night.--Male observed singing in a clump of A. magdalenae and inside a nearby curled Heliconia leaf. Female observed on unfurled Heliconia leaf. Rare at lights.

When Active at Night.--Mid to late evening (2300 to 0500 h).

Other Observations.--In the lab, several lone males were observed to deposit a regurgitated drop of clear liquid every few cm on the surface of their cages, as if marking a trail.

A male last instar nymph was captured on 17 May 1984 and molted to the adult form on 21 May. Six days latter (27 May) it was still soft to the touch and lighter in color than other adults specimens. On 4 June, two weeks after it molted, it produced a few call pulses for the first time. Subsequently, it produced slightly longer calls every day

until it began to sing the lengthy sustained call of this species in early July. It lived 5 months. Another individual lived 10 months in captivity.

Signal Analysis.--The airborne call is a loud series of regularly spaced, squeaky, high pitched zips that occur in rapid succession (Figs. 7-12a,b). To the human ear, the sounds produced are more or less continuous. Slowed, each zip consists of two rapid decay pulses (one of which is shown in Fig. 7-12c), which show some frequency modulation (Fig. 7-12d). In 10 one hour periods, 10 individuals sang without interruption for an average of 30 min 8 s (\pm 8 min 52 s) and were silent for 29 min 52 s (\pm 8 min 52 s). Pulses are paired; the duration of a pair, excluding the interpair interval 0.12 (\pm 0.02 s) (n = 79). Interpair interval is 0.15 (\pm 0.01 s) (n = 70). The individual pulses last 0.021 \pm 0.2 s (n = 20) and intrapair interval is 0.035 \pm 0.2 s (n = 20). The call is fairly pure in tone. The low and high frequencies of the call are 8.6 and 44.1 kHz, respectively. Peak frequencies in the calls of 2 animals were 14.2 and 14.1 kHz, respectively. Second and third, harmonically related peaks occurred at 28.2 and 42.2 kHz (male 1), and 28.2 and 42.3 (male 2). Call intensity in these animals was 103 dB at 7 cm and 102 dB at 3.5 cm, respectively. The duty cycle of the airborne calls (in this case calculated as the total time during which sound could be heard, including interpulse intervals and intrapair intervals) was 50.2, an

order of magnitude higher than any of the other forest katydids studied or heard on BCI.

Tremulations were examined only in males, and looked like slow 'deep knee bends'. Their length was variable (19.7 ± 15.5 s; $n = 7$). Tremulations in this species were not produced between airborne calling bouts.

I. pulchripennis males produced either airborne calls or substrateborne calls. The latter were usually produced after the insect in question experienced a disturbance (usually vibration caused by the observer), which caused it to cease calling audibly.

Males in the laboratory called between 2150 and 0400 h. The insects remained still while calling, but waved their long antennae constantly. The insects walked about their cages or groomed between calling bouts.

Comparison with Calls of Other Species.--I. pulchripennis is unusual in that pulses of its call show frequency modulation (Fig. 7-12d). This has also been described in the call of Docidocercus chlorops n. sp. from Ecuador (Morris, Klimas and Nickle, in press).

Mimetica mortuifolia Pictet
Pseudophyllinae
Fig. 7-13

Literature.--Brunner von Wattenwyl (1895); Vignon (1931); Beier (1960); Robinson (1969a).

Description.--Small-medium (males) to medium (females) long and broad winged katydid. Wings bear remarkable resemblance to leaves in shape, venation and color, and often have apical tips pointed to resemble drip-tips, hyaline patches that resemble necrotic patches, and/or irregular margins that mimic damage caused by herbivorous insects. Color of body and wings varies from individual to individual, and can be uniformly monochromatic (light brown, cinnamon, dark brown, olive, various greens) or mottled (e.g., green and yellow, brown and green). Legs often brown, even if wings and body are not, and have small blunt lateral projections that resemble irregularities on wood. Mandibles small.

Specimens Examined.--3 females and 8 males, including 82-34, 83-48, 83-140, 83-166, 83-233, 83-288, 83-322, 83-324, 84-73, 84-231, and 84-288.

Measurements.--TL: females 53.2 (\pm 5.0), males 35.7 (\pm 1.6). BL: females 31.9 (\pm 3.1), males 22.1 (\pm 1.5). LLFW: females 45.7 (\pm 3.0), males 29.1 (\pm 1.1). WLFW: females 26.4 (\pm 2.8), males 18.4 (\pm 0.9). ANT: females 90.4 (\pm 6.5), males 71. OVIP: 14.9 (\pm 0.5). WT: females 1.64 (\pm 0.4), males 0.86 (\pm 0.1).

Months Collected (as adults).--February, May, June, July, August, November.

Relative Abundance.--Uncommon.

Habitat.--Forest understory.

Diet.--Herbivorous in lab. Two individuals in the field observed eating Lantana berries.

Predators on BCI.--Not known. Do not appear in roost cullings of foliage gleaned by bats on BCI (Belwood this study, Chap. 4).

Defensive Behaviors.--Cryptic on leafy foliage of appropriate color. Also, adopt mimetic attitude (Robinson 1969a,b) on vegetation--the long antennae are held forward side-by-side on the substrate, the legs are usually folded against each other under the body, or are stretched out at 45° angle away from the body, and the head is often placed on the substrate such that the wings project upward and away from the substrate resembling a leaf. Freeze in position when disturbed during the day. Move slowly at night.

Dayroost in Cage.--Green individuals are found on the upper or lower surfaces of living vegetation; brown individuals on vegetation with dead or dying leaves, or in leaf litter on the ground.

Dayroost in Field.--not known, but presumably as above.

Location at Night.--found on low bushes (30 to 120 cm off the ground) or in the canopy of small trees (up to 4 m).

When Active at Night.--2100 to 0300 h.

Other Observations.--These insects appear to remain in the same location for about a week. A male believed to be the same individual was heard singing in the canopy of a small tree for seven consecutive evenings.

Signal Analysis.--The airborne call was recorded from three males, a green, brown, and green and yellow morph, respectively. These calls were identical (Fig. 7-13a,b), and were heard as a short series of 10 to 16 high-pitched, pure toned squeaks. At 25°, peak frequencies of the three animals were 15.8, 16.2, and 15.8 kHz, respectively. Low and high frequencies of the calls were about 6600 and 35,000 kHz. The power spectrum of the brown morph is pictured in Fig. 7-13c, but typifies the spectra of the three insects.

Slowed, each squeak consisted of a double pulse. Each pulse was 0.05 ± 0.01 s long and the interpulse interval was 0.02 ± 0.01 s. Table 7-2 summarizes call features for the three color morphs. Intensities of the brown and green males' calls, respectively, were 93 dB at 12.5 cm, and 91 dB at 20 cm.

M. mortuifolia were not observed to tremulate.

Parascopioricus exarmatus
Pseudophyllinae
(Fig. 7-14)

Description.--Similar to Scopiorinus fragilis (this chapter), but wings wider and more oval in shape.

Specimens Examined.--2 females, 1 male, including 83-30, 84-138, 84-228.

Measurements.--TL: females 39.9 (± 0.4), male 34.7.
BL: females 35.5 (± 3.0), male 27.3. LLFW: females 32.5,

Table 7-2.--Comparisons of airborne call features in three color morphs of the leaf-mimicking katydid Mimetica mortuifolia. (n) is number of calls or pulses examined in each category.

Color morph	GREEN/YELLOW	BROWN	GREEN
Length (s) of calling bout (n)	2.1 ± 0.7 (4)	1.2 ± 0.7 (8)	1.5 ± 0.5 (15)
Double pulses per calling bout (n)	15.5 ± 5.7 (4)	9.8 ± 4.8 (8)	14.1 ± 4.3 (15)
Pulse length (s) (n)	0.05 ± 0.01 (62)	0.05 ± 0.01 (78)	0.05 ± 0.01 (211)
Interpulse interval (s) (n)	0.02 ± 0.01 (15)	0.02 ± 0.01 (15)	0.02 ± 0.01 (15)
Interpulse-pair interval (s) (n)	0.14 ± 0.01 (15)	0.14 ± 0.02 (15)	0.14 ± 0.01 (15)

male 29.4. WLFW: females 12.2 (\pm 0.8), male 10.1. ANT: females 51.9 (\pm 8.1). OVIP: 13.6 (\pm 0.1). WT: females 1.3 (\pm 0.1).

Months Collected (as adults).--April, May, June, November.

Relative Abundance.--Uncommon.

Habitat.--Forest understory, also seen at forest edge.

Diet in Lab.--Herbivorous.

Defensive Behavior.--Both males and females produce a loud disturbance call when handled.

Dayroost in Cage.--On top surface of green leaves, in a manner similar to that described for Scopiorinus fragilis (Robinson 1969b).

Location at Night.--On leaf surfaces in forest understory.

When Active.--1600 to 0530 h

Signal Analysis.--The airborne call of P. exarmatus was heard as series of noisy, buzzy zips (Figs. 7-14a,b) that are produced continually and at regular intervals for hours at a time. Slowed, each call is a train of 10 to 20 pulses (Fig. 7-14c). The first pulse (Fig. 7-14d) rises in amplitude relatively slowly compared to most of the subsequent pulses and is lower in overall amplitude. The second pulse (Fig. 7-14e) also slowly rises in amplitude, but is about twice the amplitude of the preceeding one. The remaining pulses (Fig. 7-14f) have relatively steeper onsets and

constant amplitudes. The last pulse is similar to the first. At 26°C, 17.9 ± 8.9 such calls were produced per 5 min period ($n = 36$) in a total of three animals. Calls lasted 0.33 ± 0.01 s. The low and high frequencies of the call are 12.6 and 27.2 kHz, respectively. Peak frequencies in the calls of two animals were 17.6 and 18.2 kHz, respectively. Call intensity in 2 animals was 105 dB at 10 cm and 108 dB at 10 cm, respectively. The duty cycle of the airborne calling song was 1.98.

Substrateborne calls were not observed in males or females of this species.

Males in the laboratory called between 1600 and 0330 h. Males remained perfectly still and called from both horizontal and vertical surfaces. Occasionally, an individual interrupted its calling to change its orientation, usually 180 degrees. These katydids continued to sing in a flight cage in the presence of flying bats, Tonatia silvicola that produce echolocation calls with peak frequencies of 79.1 ± 9.0 kHz (range 56.4 to 92.4 kHz) (Belwood, this study, Fig. 5-2).

Pristonotus tuberosus (Stål)
Pseudophyllinae
(Fig. 7-15)

Literature.--Stål (1875); Brunner von Wattenwyl (1895); Griffini (1896b); Saussure and Pictet (1898); Bruner (1915); Hebard (1927); Sjöstedt (1933); Beier (1954, 1962).

Description.--Large cylindrical, dark colored and long winged. Uniformly mottled dark and light brown tortoise shell-like pattern. Some specimens have considerable mossy green patches on the body and wings. A cream facial stripe extends from base of each antenna to the clypeus. Numerous small dark cuticular protuberances on pronotum. Distal margin of tegmina rounded and the numerous veins along costal margin and around humeral angle of wing are green. Ovipositor straight, rigid, and bladelike, but with small hump on dorsal margin; proximal third (to half) buff, distal two-thirds (to half) dark brown and serrated on dorsal margin.

Specimens Examined.-- 5 females, 4 males, including 83-142, 83-209, 83-278, 83-281, 83-289, 83-311, 84-202, 84-263, 84-361.

Measurements.--TL: females 82.4 (± 3.3), males 69.9 (± 1.1). BL: females 61.2 (± 11.4), males 57.1 (± 3.8). LLFW: females 66.8 (± 2.6), males 56.3 (± 1.9). WLFW: females 13.4 (± 1.1), males 13.1 (± 1.4). ANT: females 177, males 165. OVIP: 34.4 (± 1.8). WT: females 7.5 (± 1.9), males 6.8 (± 0.7).

Months Collected (as adults).--March, May, June, July, August, September, October, November.

Relative Abundance.--Uncommom.

Habitat.--Forest understory.

Diet in Lab.--Herbivorous.

Predators on BCI.--Not known.

Defensive Behaviors.--Regurgitate fluid from crop and males produce distress squawks when handled.

Dayroost in Cage.--Not known.

Dayroost in Field.--Not known.

Location at Night.--On tree trunks.

When Active at Night.--Early, mid and late evening.

Other Observations.--A male in captivity produced a three-lobed, spermatophore when mated to a female. It measured 11 by 13 mm, weighed 0.64 g, and represented 9.5% of the male's weight.

Signal Analysis.--The airborne call is heard as a single, short, loud, and noisy, tick (Fig. 7-15a,b). This is followed by a long silent bout before the call is repeated. Slowed, the tick consists of a single pulse (Fig. 7-15c), which is characterized by a gradual onset before it reaches maximum amplitude and rapid decay. At 25°C, 6.7 ± 4.7 calls were produced per 5 min period ($n = 86$) in 6 animals. Calls lasted 0.06 ± 0.02 s ($n = 12$). The low and high frequencies of the call were 4.2 and 32.0 kHz (check), respectively. Peak frequencies in the calls of 2 animals were 10.0 and 10.2 kHz. Call intensity in calls from three animals was 113 dB at 18.4 cm, 97 dB at 7 cm, and 110 dB at 35 cm, respectively. Duty cycle of the airborne call was 0.13.

Substrateborne calls were observed, but not studied, in females. The occurrence of tremulations in this species should be investigated further.

Males in the laboratory called between 2130 and 0300 h. They remained perfectly still while they called.

Scopiorinus fragilis (Hebard)
Pseudophyllinae
(Fig. 7-16)

Literature.--Hebard (1927); Beier (1960); Robinson (1969b); Belwood (this study, Chap. 6); Morris and Beier (1982) describe the airborne calls of the closely related S. impressopunctatus, S. carinulatus, and S. mucronatus.

Description.--Small-medium, slender, fragile, long winged katydid. Uniformly green with dull finish. Antennae about four times body length. Pronotum with occasional yellow flecks. Tegmina long and narrow and slightly convex, with rust or yellow flecks along costal wing margins. Limbs long and slender with small black spines on lateral surfaces of front femora.

Specimens Examined.-- 3 females, 3 males, including 83-74, 83-296, 84-8, 84-46, 84-49.

Measurements.--TL: females 37.7 (\pm 2.1), males 35.5 (\pm 4.1). BL: females 32.0 (\pm 1.8), males 33.7 (\pm 4.7). LLFW: females 30.8 (\pm 0.9), males 28.0 (\pm 3.0). WLFW: females 6.3 (\pm 0.3), males 5.7 (\pm 1.1). ANT: females 113.4 (\pm 13.0),

males 161 (± 10.0). OVIP: 9.2 (± 0.3). WT: females 0.9 (± 0.01), males 0.6.

Months Collected (as adults).--March, April, July, August, September, October.

Relative Abundance.--Uncommon.

Habitat.--Forest understory; sometimes forest edge.

Diet in Lab.--Herbivorous. Observed to eat fungus on a rotting piece of wood collected on the forest floor.

Predators on BCI.--Its calls were used to attract foliage gleaning bats, but these insects do not seem to be important in the diets of two such bats that were studied on BCI (Belwood this study, Chap. 4).

Defensive Behaviors.--Both males and females produce a disturbance call when handled. Males stop calling and adopt a characteristic posture when disturbed (Robinson 1969b). At this time, the fore and hind legs are extended maximally, anterior and posterior, respectively, and the antennae are projected forward along the insect's midline. The substrate is also gripped tightly.

Dayroost in Cage.--Exposed on the upper surface of leaves, as described by Robinson (1969b).

Dayroost in Field.--As above (Robinson 1969b).

Location at Night.--On upper surfaces of leafy vegetation.

When Active.--1600 to 0400 h.

Signal Analysis.--The airborne call of S. fragilis was heard as a series of regularly spaced, single, soft, high-pitched ticks (Fig. 7-16a,b). They are faint and to the human ear resemble the ticking of a watch. Slowed, each tick consists of about six pulses that occur in rapid succession (Fig. 7-16c). Overall, the first three rise gradually in amplitude. The next two are maximum amplitude and each has a sharp transient onset. The last pulse decreases rapidly in amplitude. The call of this animal is remarkable in its regularity and duration. Members of this species have been heard to call for up to five hours at a time. 213.2 ± 27.2 ticks were produced per 5 min period ($n = 36$) in 3 animals. Ticks lasted 0.064 ± 0.001 s ($n = 94$) and the interval between successive ones was 1.2 ± 0.2 s. The low and high frequencies of the call are 14.4 and 39.6 kHz, respectively. Peak frequencies in the calls of 3 animals were 24.8, 25.0, and 25.2 kHz. Call intensity in 2 animals was 96 dB at 15 cm, and 103 dB at 9 cm, respectively. The duty cycle of the airborne call is 4.55.

Occasional substrateborne calls or tremulations were observed in males. These occurred sporadically, and were not produced by all the individuals that were observed. The tremulations were very shallow vertical body vibrations and were almost unnoticeable to the human eye. The number of tremulations produced per 5 min period was not examined.

Males in the laboratory called between 1600 and 0300 h. These animals remained perfectly still, for up to 5 h at a time when they called. What is believed to be one individual was heard calling in the field, in the same spot in dense vegetation on four consecutive days, but could not be located. One male in captivity was heard to sing for several hours on the day after he was observed to mate with a conspecific female.

Comparison with Calls of Conspecifics.--Morris and Beier (1982) describe the calls of three species of Scopiorinus from Costa Rica; two (S. carinulatus, S. mucronatus) occur in cloud forest (Monteverde) and the other (S. impressopunctatus) in the lowlands (La Selva). All four species are slender and have long antennae (up to five times body length). As in this study, Morris and Beier never found Scopiorinus stridulating in the field.

The calls of the four species are compared in Table 7-3. This shows that the calls of the two lowland forest species are similar to the call of one of the cloud forest species (S. mucronatus), in that all are faint high-pitched ticks. The call of the remaining cloud forest species (S. carinulatus) differs; it is a "sustained buzz" rather than a tick. The call duty cycles for S. fragilis and S. impressopunctatus are low (< 5%). The calls of the Costa Rican species appear to be less intense than that of the Panamanian species.

Table 7-3.--Comparison of airborne calls in four species of Central American Scopiorinus katydids (Tettigonidae: Pseudophyllinae).

SPECIES	<u>S. fragilis</u>	<u>S. impressopunctatus</u>	<u>S. mucronatus</u>	<u>S. carinulatus</u>
BODY LENGTH	3.5 cm	3 cm	3 cm	3 cm
COLLECTION LOCALITY	BCI, Panama	La Selva, C.R.	<-----Monteverde, Costa Rica----->	
HABITAT	<-----lowland forest----->		<-----cloud forest----->	
CALL DESCRIPTION	<-----Regularly spaced, faint high-pitched ticks-----> (like ticking of a watch)			
CALL REP. RATE	1.4/s	1.4/s	1.2/s	-----
CARRIER FREQUENCY	25 kHz	29 kHz	-----	28 kHz
DUTY CYCLE	4.55%	3.0%	-----	-----
INTENSITY	96 dB at 15 cm	84 dB at 6 cm	96 dB at 5 cm	88 dB at 5 cm

Unknown Pseudophylline "a"
(Fig. 7-17)

Literature.--unknown

Description.--Medium, slender, elongate katydid. Eyes, head, antennae, legs and body mottled pattern in light taupe browns. Cerci light cream. Veins on tegmina cream except for anal area where they are yellow. Cells between veins brownish black. Numerous thin black lines and small black dots on pronotum. Dark brown patch on gena below each eye. Ovipositor stiff and bladelike, with slight upward curve. Dorsal margin serrated.

Specimens Examined.-- 4 females, 5 males, including 83-194, 83-230, 83-291, 83-301, 83-310, 84-51, 84-83, 84-84, 84-155.

Measurements.--TL: females 51.6 (± 3.0), males 43.4 (± 1.6). BL: females 37.9 (± 3.5), males 40.0 (± 3.5). LLFW: females 36.6 (± 1.5), males 34.4 (± 1.2). WLFW: females 7.0 (± 0.2), males 6.4 (± 0.4). ANT: females 140.3 (± 12.6), males 114.2 (± 12.1). OVIP: 17.3 (± 0.8). WT: females 1.8 g (± 0.4) g, males 1.6 (± 0.3) g.

Months Collected (as adults).--February, March, April, August, September, October.

Relative Abundance.--Uncommom.

Habitat.--Forest understory.

Diet.--Herbivorous.

Known Predators on BCI.--Not known.

Defensive Behaviors.--Raises its wings in a defensive posture like A. curvidens (p. 149). Males produce distress squawk when handled. Dayroost in concealed places.

Dayroost in Cage.--In curled dead leaves, in cracks and crevices on woody structures.

Dayroost in Field.--Not known.

Location at Night.--Occasionally at ultraviolet lights in clearing.

When Active at Night.--Early to mid evening (1700 to 2400 h).

Other Observations.--When mated to a female, a captive male produced a large four lobed-spermatophore that measured 5 by 6 mm. It weighed 0.42 g, approximately 25.32 % of the male's weight.

Signal Analysis.--The airborne call is a single faint, but raspy tick. At 26° C, 5.1 (\pm 2.7) ticks were produced per 5 min period (n = 24) by 2 animals. Ticks lasted 0.1 s (n = 10). The low and high frequencies of the call are 12.0 and 40.2 kHz, respectively. Peak frequency in the calls of animal was 17.2 kHz, with a smaller, harmonically related peak at 37.4. Call intensity was not measured.

Substrateborne calls or tremulations were observed in males and females of this species, but were not recorded.

Males in the laboratory were observed to call between 2300 and 2450 h.

Unknown Pseudophylline "b"
(Fig. 7-18)

Literature.--Belwood (this study, Chap. 4).

Description.--Small, chubby but delicate, cylindrical katydid. Wings about as long as body and slightly convex. Entire body light taupe color with subtle mottled pattern. Finish dull. On some specimens the costal wing margin is cream or green. Stridulatory field in males visible as prominent dark brown triangle. Ovipositor curves upward, lacks serrations, and has margins darker than center.

Specimens Examined.--8 females, 2 males, including 83-119, 83-154, 83-155, 83-220, 83-235, 84-17, 84-50, 84-170, 84-183, 84-270.

Measurements.--TL: females 36.6 (± 0.9), males 26.9 (± 2.2). BL: females 27.3 (± 1.3), males 25.4 (± 4.3). LLFW: females 22.1 (± 0.6), males 19.9 (± 0.2). WLFW: females 6.4 (± 0.7), males 5.9 (± 0.2). ANT: females 109.4 (± 25.5), males 140.0 (± 0.9). OVIP: 13.3 (± 0.4). WT: females 0.9 (± 0.2), males 0.9.

Months Collected (as adults).--March, April, May, July, August, September.

Relative Abundance.--Uncommon.

Habitat.--Forest understory. Two specimens taken in vegetation at forest's edge.

Diet in Lab.--Herbivorous.

Predators on BCI.--Constitute about 10% (by number) and 4% (by weight) of the diet of the foliage gleaning bat Micronycteris hirsuta over a two year period on BCI (Belwood this study, Chap. 4). Probably also birds that forage on insects that dayroost in or leaves in the forest (Greenberg and Gradwohl 1980; Gradwohl and Greenberg 1982, 1984).

Defensive Behaviors.--Dayroost in concealed places.

Dayroost in Cage.--In curled leaves and in crevices on woody substrates.

Dayroost in Field.--One found roosting in a curled leaf 30 cm off the ground in forest.

Location at Night.--Incandescent lights.

When Active at Night.--Early evening (1700 to 2400 h) and 0430 to 0600h. A caged male was observed to return to its dayroost (a curled dead leaf) at 0144 h after several hours of singing. It re-emerged at 0423 h and resumed singing until sunrise.

Other Observations.--None.

Signal Analysis.--The airborne call was heard as a successive series of short, single, high pitched ticks (Fig. 7-18a,b). Slowed, each tick consists of two pulses, the first of which is only about one-half the length of the second (Fig. 7-18c). The first pulse has a rapid onset and decay, and its amplitude remains more or less constant. Onset and decay in the second pulse are more gradual. At 27°C, 18.75 ± 2.1 such calls were produced per 5 min period

($n = 24$) in 2 animals. They lasted 2.7 ± 0.3 s ($n = 7$), and the average number of double pulses per call was 8.6 ± 0.1 ($n = 7$). The length of the double pulse was 0.04 ± 0.005 s ($n = 60$), and the silent interval separating the double pulses was 0.3 ± 0.06 s ($n = 50$). The low and high frequencies of the call were 14.2 and 24.1 kHz, respectively. The peak frequency of the calls of 1 animals was centered at 17.4 kHz. Call intensity was 105 dB at 7 cm. The duty cycle of the airborne calling song was 2.2.

Substrateborne calls were not observed in males or females of this species, but should be investigated further.

Males in the laboratory were observed to call between 1700 and 0200 h and just before dawn. These animals remained still while they called, although they waved their antennae around their bodies in constant motion.

Xestoptera cornea Brunner von Wattenwyl
Pseudophyllinae
(Fig. 7-19)

Literature.--Brunner von Wattenwyl (1895); Saussure and Pictet (1898); Hebard (1927, 1933); Beier (1960); Belwood this study (Chap. 4).

Description.--Medium-sized, long winged, oval katydid. Face, antennae and body uniform deep forest green. Eyes tan. Tegmina convex and very shiny with area abutting costal margin washed in white. Hind wings pinkish. In males, stridulatory field and costal tegminal margins rusty brown.

Ovipositor long, green, stiff, but not bladelike (see Beier 1960).

Specimens Examined.-- 5 females, 3 males, including 83-146, 83-239, 84-292, 84-308, 84-314, 84-325, 84-330.

Measurements.--TL: females 54.2 (\pm 4.3), males 41.7 (\pm 1.5). BL: females 34.8 (\pm 4.9), males 34.5 (\pm 1.0). LLFW: females 37.4 (\pm 1.3), males 33.6 (\pm 0.5). WLFW: females 12.8 (\pm 0.5), males 11.1 (\pm 0.8). ANT: females 110 (\pm 8.5). OVIP: 23.3 (\pm 0.8). WT: females 3.6 (\pm 0.2), males 2.4 (\pm 0.3).

Months Collected (as adults).--June, July, August, September, October.

Relative Abundance.--Common, but seasonal--restricted to mid wet season. Most abundant in late June, July and August.

Habitat.--Forest understory and canopy.

Diet in Lab.--Herbivorous.

Predators on BCI.--This is a major food for the foliage gleaning bat Micronycteris hirsuta (Belwood this study, Chap. 4). It constitutes 17.1% of the diet by number and 25.8% by volume. In 1984, the first X. cornea was seen at ultraviolet lights on 21 June. Wings of this species began to appear in bat roosts in large numbers on 24 June.

Defensive Behaviors.--Females produce a disturbance call when handled.

Dayroost in Cage.--On the under surface of green leaves.

Dayroost in Field.--Unknown, but presumably as above.

Location at Night.--Males were heard singing in the forest canopy (at least 10 m high). Females and males have also been seen from ground level to 3 m above ground. One female was found on the ground with soil on her ovipositor, indicating that oviposition may take place in soil on the ground. Occasionally at lights.

When Active at Night.--Early to late evening; 2000 to 0330 h.

Other Observations.--Individuals appear to emerge as adults synchronously and in large numbers.

Signal Analysis.--The airborne call consists of one, two, or three (usually two) loud and raspy zips that are produced in rapid succession. They are broadband, and have considerable energy in the audio range (Figs. 7-19a,b). Slowed, each zip is a short train of seven to ten major pulses, each of which is followed by a minor pulse (Fig. 7-19c).

In the field and laboratory, males chorused (Greenfield and Shaw 1983) in response to one another. Therefore, only lone males were studied in the lab. Six animals produced 4.4 ± 3.5 calls per 5 min period ($n = 71$). Zips lasted 0.5 ± 0.1 s ($n = 30$). The low and high frequencies of the zips were 7.8 and 52.6 kHz, respectively. Peak frequencies in

the calls of 3 animals were 27.0, 27.4, and 28.1 kHz. Call intensity in one animal was 91 dB at 27 cm. The duty cycle of the airborne calls was 1.47.

Very faint tremulations were observed in males, and only when they shared a substrate with a responding (tremulating) female. Tremulations were not recorded. In 6 males, $5.0 (\pm 7.9)$ tremulations were produced per 5 min period ($n = 48$). Tremulations were only produced when the insects were on wood or another rigid substrate (not leaves).

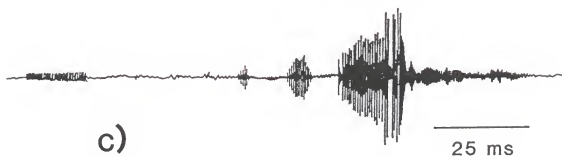
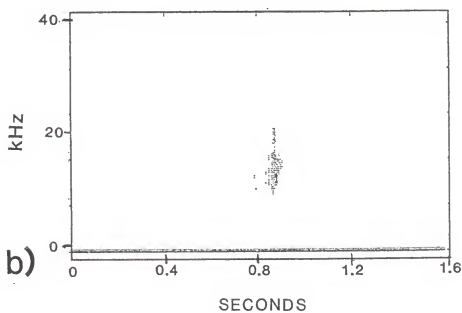
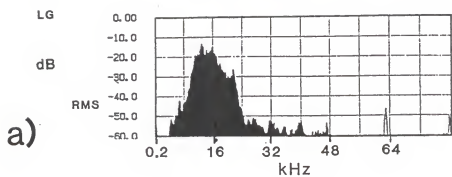
Most males were observed to call between 2000 and 2400 h. These animals do not move when they call although occasionally they may change their body orientations by 90 or 180 degrees.

Discussion

Airborne Calls

Acoustic behavior (sound production and audition) has been studied in detail in relatively few katydid species. In this respect, temperate species that are plentiful, easily accessible, active before midnight, easy to maintain in the laboratory, and that have conspicuous (audible and sustained) airborne calls have received the most attention (e.g., the numerous studies cited in Alexander 1960 and Gwynne and Morris 1983). However, some tropical species

Fig. 7-4.--Calls of Acanthodis curvidens. (a) to (c) are airborne song: (a) power spectrum, (b) audiospectrogram, and (c) oscillogram. (d) is temporal pattern of the bounce train of two tremulation bouts. The bout on the right is complete.



ACANTHODIS CURVIDENS

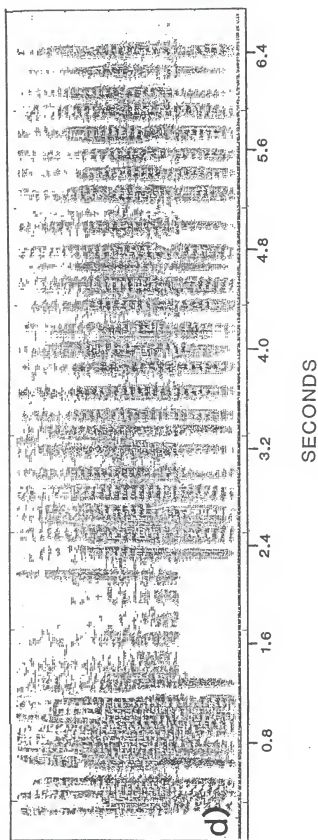
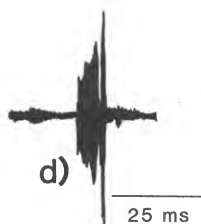
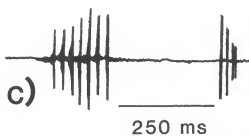
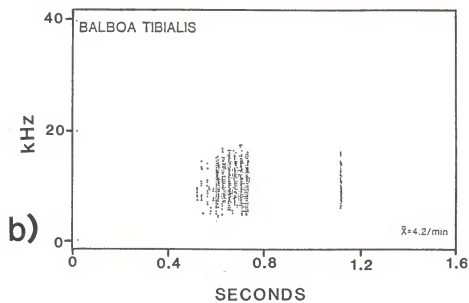
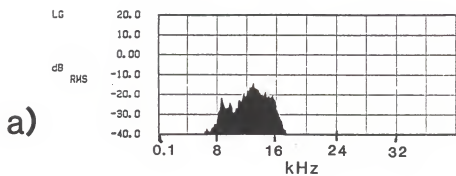


Fig. 7-4 (continued).

Fig. 7-5.--Calls of Balboa tibialis. (a) to (d) are airborne song: (a) power spectrum, (b) audiospectrogram, (c) oscillogram of the two pulse trains of call, and (d) detail of one pulse in the first pulse train of oscillogram. (e) and (f), respectively, are temporal patterns of male and female tremulation call bouts.



BALBOA TIBIALIS

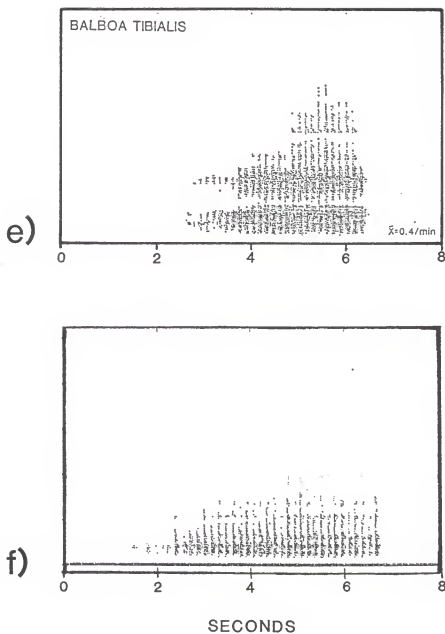
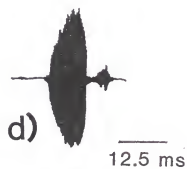
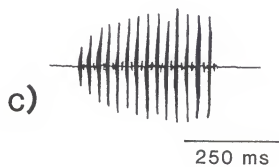
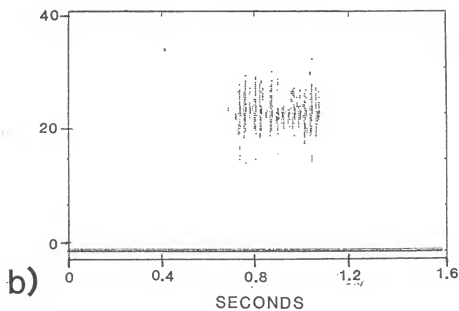
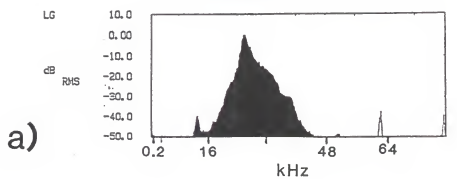


Fig. 7-5 (continued).

Fig. 7-6.--Calls of Cocconotus wheeleri. (a) to (d) are airborne song: (a) power spectrum, (b) audiospectrogram, (c) oscillogram, and (d) enlargement of one major pulse followed by minor pulse. (e) is temporal pattern of the male's double-bounce substrate call.



COCCONOTUS WHEELERI

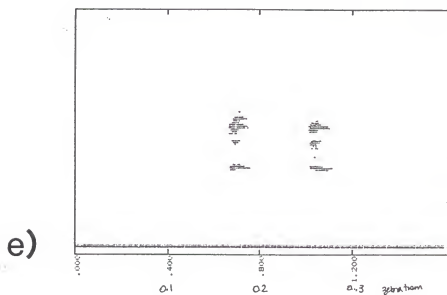
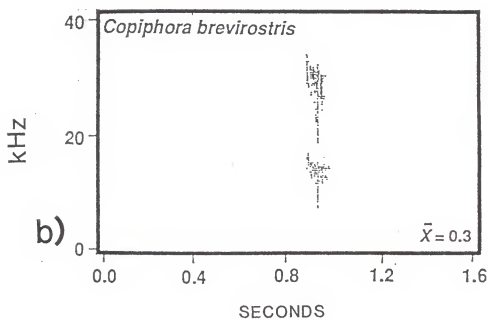
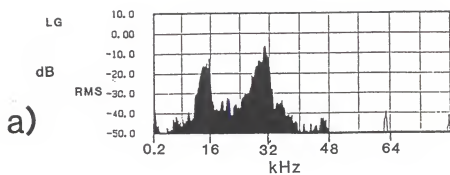


Fig. 7-6 (continued).

Fig. 7-7.--Calls of Copiphora brevirostris. (a) to (c) are airborne song: (a) power spectrum, (b) audiospectrogram, and (c) oscillogram of the "zip" that is the call. (d) and (e) are temporal patterns of the tremulation signal measured indirectly (from insect in cage) and directly (from leaf on which insect sat), respectively. See text for explanation. (e) courtesy of Dr. G.K. Morris, University of Toronto.



COPIPHORA BREVIROSTRIS

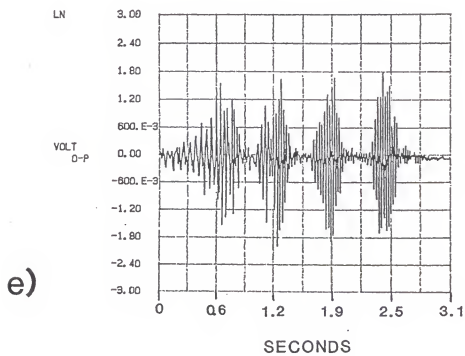
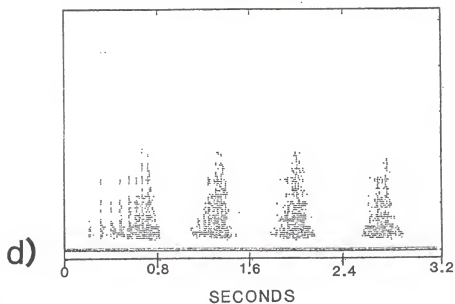
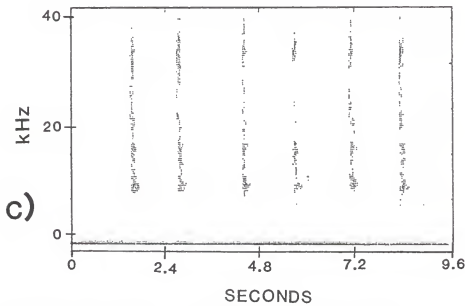
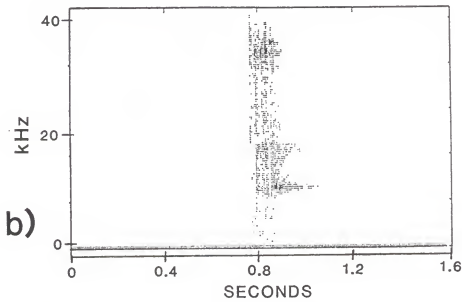
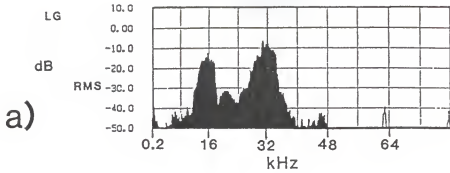


Fig. 7-7 (continued).

Fig. 7-8.--Airborne calling song of Copiphora nr brevirostris: (a) power spectrum, (b) individual pulse train (note), (c) some of the four to nine notes that constitute the song, and (d) oscillogram of one note of call.



COIPHORA nr BREVIROSTRIS

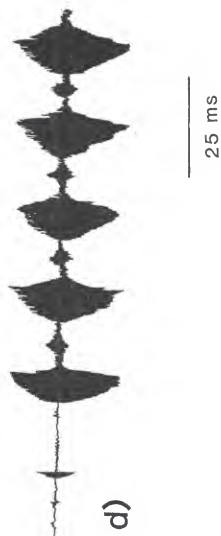
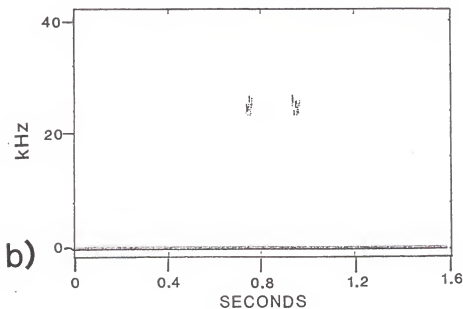
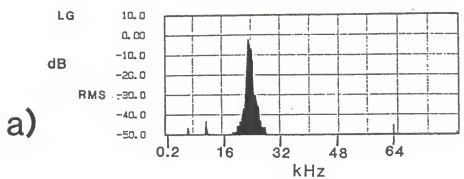


Fig. 7-8 (continued).

Fig. 7-9.--Calls of Docidocercus gigliotosi. (a) to (c) are airborne calls: (a) power spectrum, (b) audiospectrogram, and (c) oscillogram of one pulse. (d) and (e), respectively, are temporal patterns of the male's substrateborne call as recorded indirectly in a cage (with a microphone and tape recorder), and directly with an accelerometer. (e) cortesey of Dr. G.K. Morris, University of Toronto.



DOCIDOCERCUS GIGLIOTOSI

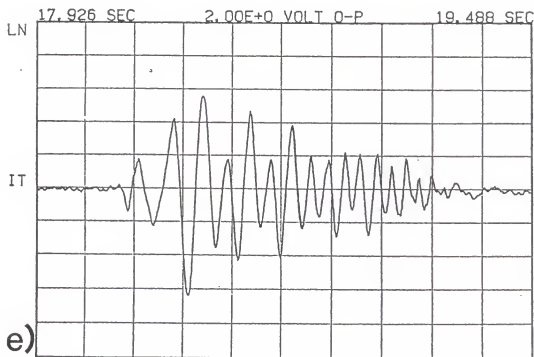
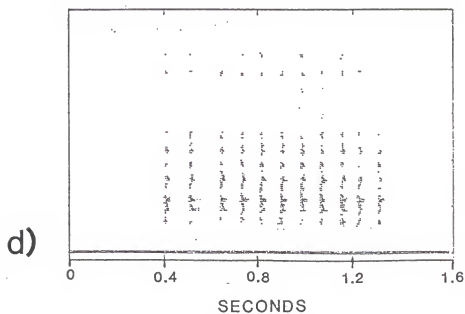
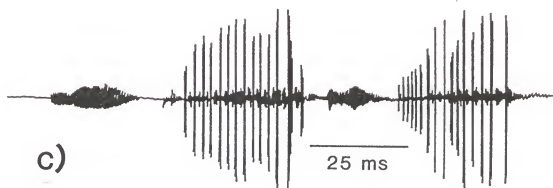
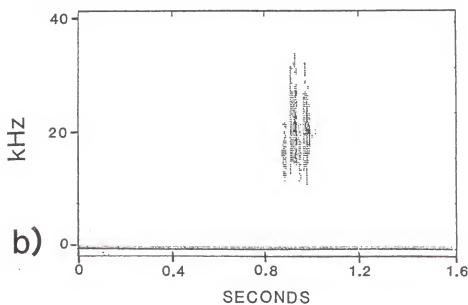
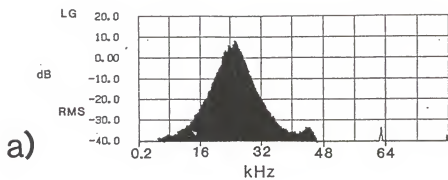


Fig. 7-9 (continued).

Fig. 7-10.--Calls of Eucocconotus camerami. (a) to (c) are airborne song: (a) power spectrum, (b) audiospectrogram, and (c) oscillogram. (d) is temporal pattern of a male's tremulation signal.



EUCOCCONOTUS CAMERANI

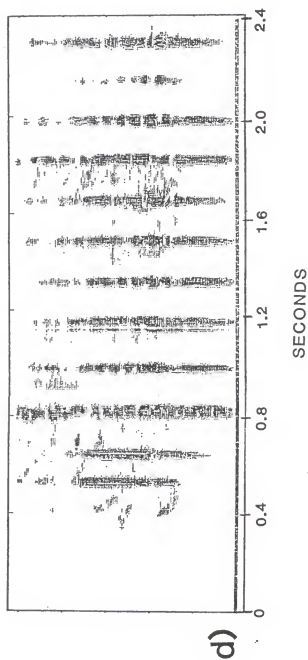
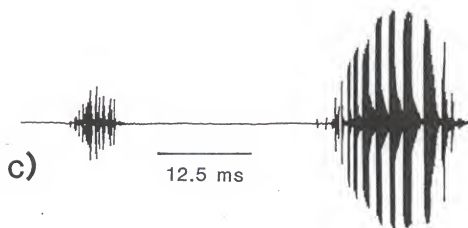
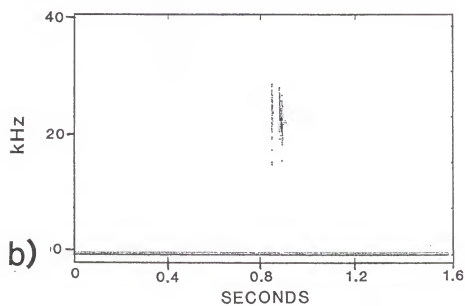
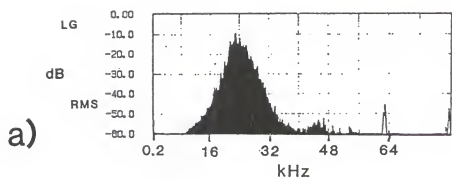


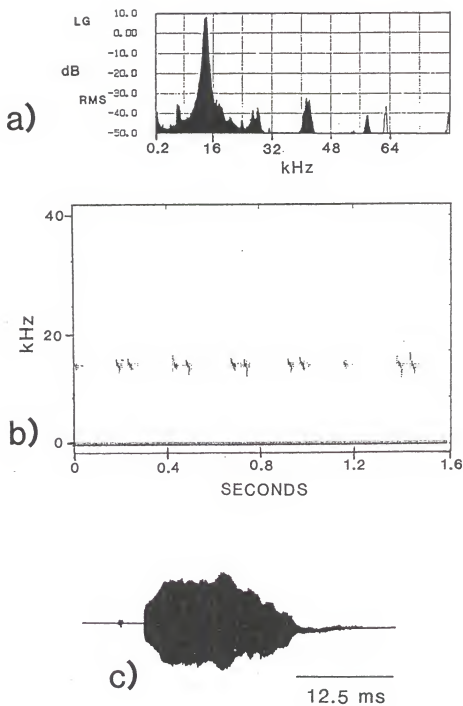
Fig. 7-10 (continued).

Fig. 7-11.--Airborne calls of Idiarthron major: (a) power spectrum, (b) audiospectrogram, and (c) oscillogram of the two pulse trains that constitute one call.



IDIARTHRON MAJOR

Fig. 7-12.--Airborne calls of Ischnomela pulchripennis: (a) power spectrum, (b) audiospectrogram of 12 pulses, (c) oscillogram of one pulse, and (d) slowed tape of double pulse showing frequency modulation in each pulse.



ISCHNOMELA PULCHRIPENNIS

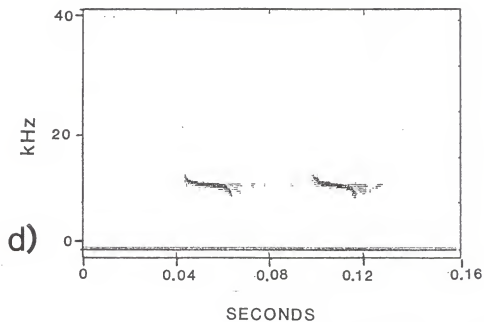
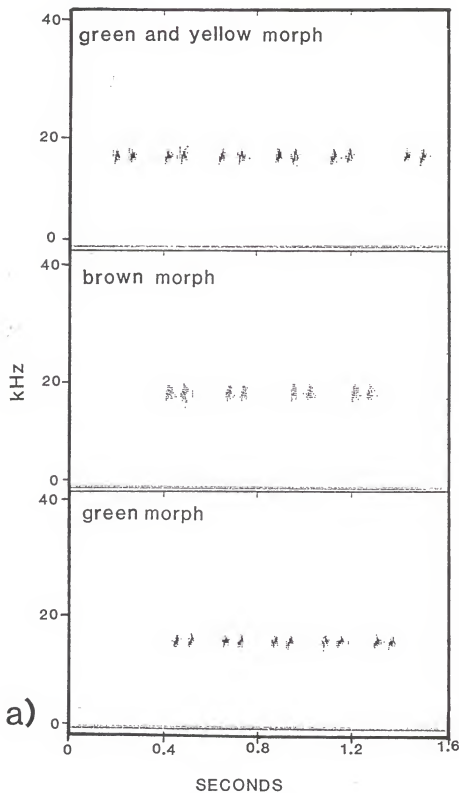


Fig. 7-12 (continued).

Fig. 7-13.--Airborne calling songs of three color morphs (green and yellow, brown, and green) of the leaf-mimicking katydid Mimetica mortuifolia: a) audiospectrograms, b) oscillograms of the double pulse, and c) power spectrum of the call of the brown morph. c) is typical of all three morphs.

MIMETICA MORTUIFOLIA



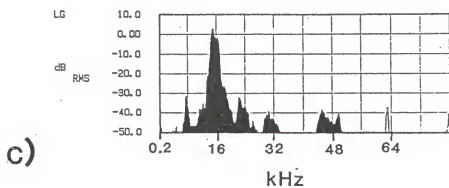
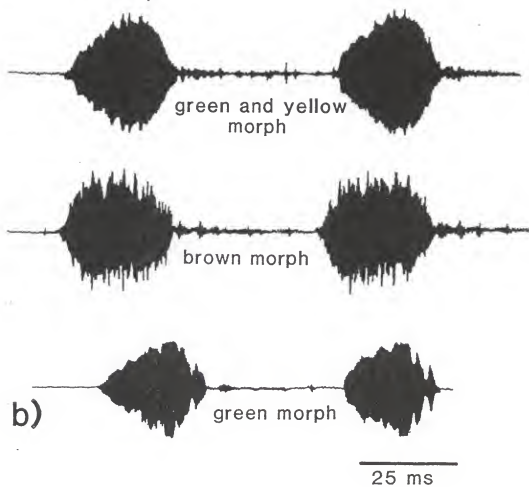
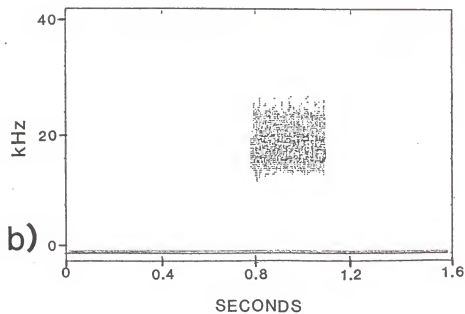
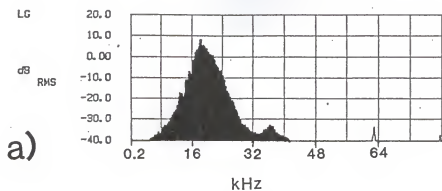


Fig. 7-13 (continued).

Fig. 7-14.--One airborne calling song of Parascopioricus
exarmatus: (a) power spectrum, (b) audiospectrogram, (c)
oscillogram, and (d-f) enlargements of individual pulses in
oscillogram showing fine structure.



PARASCOPIRICUS EXARMATUS

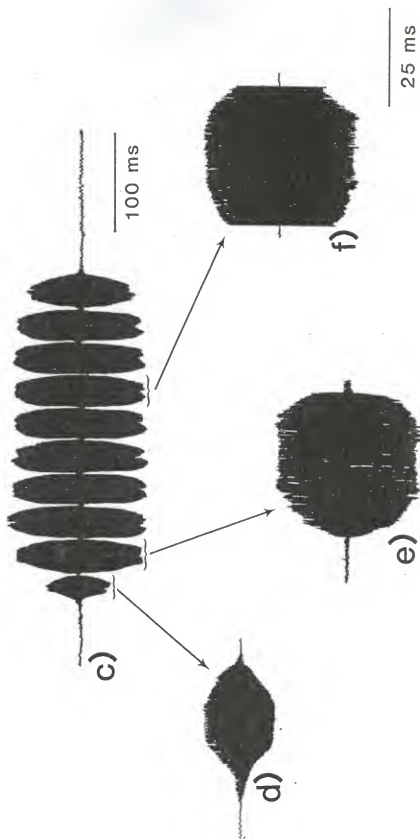
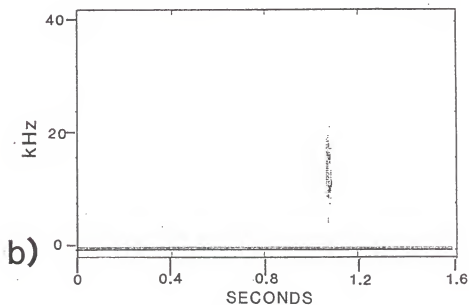
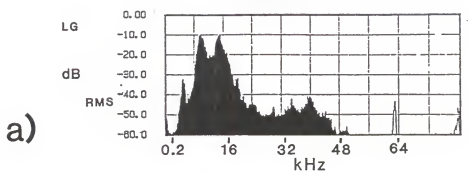


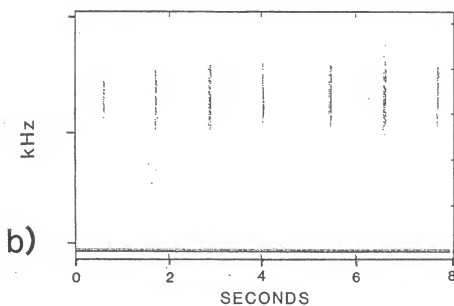
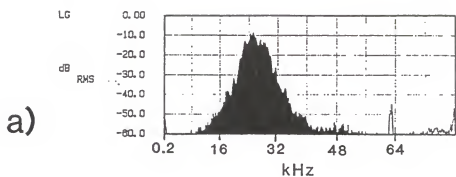
Fig. 7-14 (continued).

Fig. 7-15.--One airborne calling song of Pristonotus
tuberosus: (a) power spectrum, (b) audiospectrogram, and (c)
oscillogram.



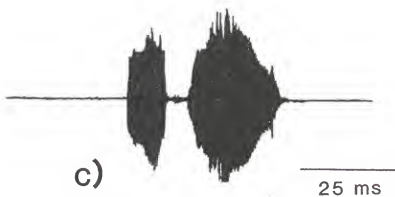
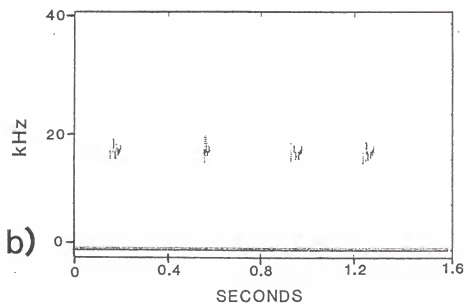
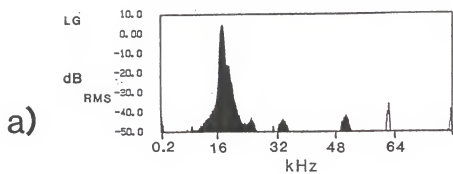
PRISTONOTUS TUBEROSUS

Fig. 7-16.--Airborne calling song of Scopiorinus fragilis:
(a) power spectrum, (b) audiospectrogram of seven pulse
trains ("ticks"), and (c) oscillogram of one "tick". The
tick consists of a train of six to eight pulses and is
repeated at regular intervals (b) for hours at a time.



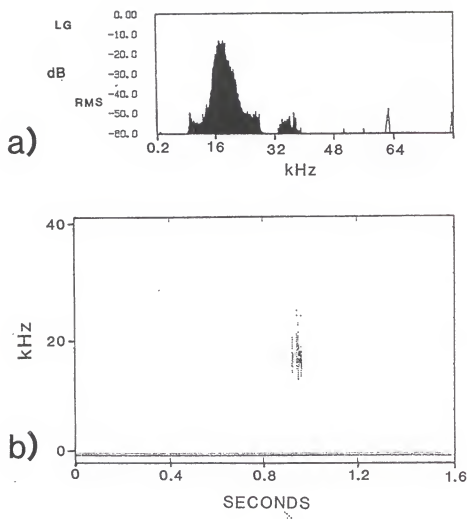
SCOPIORINUS FRAGILIS

Fig. 7-17.--Airborne calling song of unknown pseudophylline
"a": (a) power spectrum and (b) audiospectrogram.



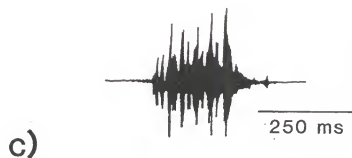
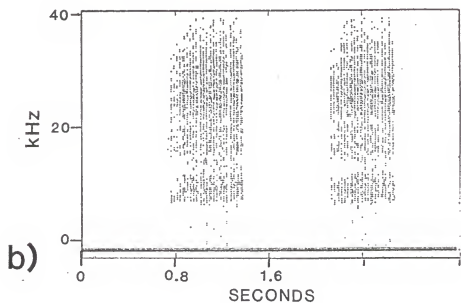
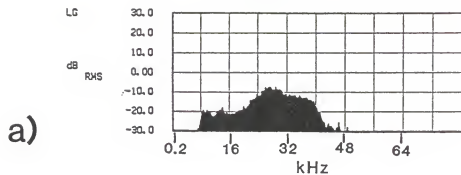
UNKNOWN PSEUDOPHYLLINE "a"

Fig. 7-18.--Airborne calling song of unknown pseudophylline "b": (a) power spectrum, (b) audiospectrogram of four "ticks" of call, and (c) oscillogram of the two pulses that constitute a tick. Seven to nine ticks make up a call.



UNKNOWN PSEUDOPHYLLINE "b"

Fig. 7-19.--Airborne calling song of Xestoptera cornea: (a) power spectrum, (b) audiospectrogram of two "zip" call, and (c) oscillogram of one zip of call.



XESTOPTERA CORNEA

that share these characteristics have also been studied (e.g., Walker and Greenfield 1983; Greenfield 1983, 1988).

Calling songs have been described for only 20 of the more than 1000 (Beier 1960, 1962) katydid species that have been described in the New World. For the most part, these occur mainly in densely forested areas and are difficult to study. Despite this, Morris and Beier (1982) and Morris, Klimas and Nickle (in press) have described the airborne calling songs of 10 species from Costa Rica and nine from Ecuador, respectively. The results presented here increase the number of species whose songs have been described to about 36. Also described here are the tremulation signals of six species and the calling songs of two copiphorine species. Although the airborne calls of males of an additional 20 phaneropterine katydid species and one agraeciine were also recorded as part of this study, these results will be presented elsewhere.

The calls of most of the Latin American pseudophyllines studied to date share several features. They are all short (usually < 1 s) and infrequently produced (every few seconds to every few minutes). In addition, they emphasize high and/or ultrasonic frequencies (> 20 kHz), and their duty cycles are extremely low. In the Panamanian species studied here, with the exception of *I. pulchripennis* (see below), the proportion of time male katydids spent singing ranged from 0.06% to 4.55%. Similarly, low duty cycles, short

sporadic calls and high pitched carrier frequencies also typify the calls of pseudophyllines from Amazonian Peru, twenty species of which were recently recorded from forested near Iquitos (Belwood, Nickle and Castner, unpublished data). In contrast, the duty cycles of Panamanian Neoconocephalus, copiphorine katydids that occur in BCI's grassy clearings range from 30 to 50% (Belwood, unpublished data), and the call of the cricket Gryllus campestris is about 23% (Morris and Beier 1982:297).

Short sporadic airborne calls in Latin American pseudophylline katydids appear to be an anti-predator response to acoustically orienting predators--most notably the foliage gleaning bats (FGB) (Chiroptera: Phyllostomidae: Phyllostominae) with which these katydids are sympatric, and which use the airborne calling songs of these insects to locate prey (Tuttle, Ryan and Belwood 1985; Belwood this study, Chap. 6). FGB are plentiful in the forested areas inhabited by the katydids discussed here (Belwood, personal observation), and they glean insects, including large numbers of katydids (Wilson 1971; LaVal and LaVal 1980a; Belwood this study, Chap. 4), from the ground, leaves, twigs, and other substrates.

I. pulchripennis appears to be the one 'exception' to the 'rule' that all forest pseudophyllines on BCI call sporadically, as its duty cycle is about 50%. This is possible because the insect sings from large (> 2 m) ter-

restrial bromeliads, which are covered with long (> 1 cm) sharp spines that could injure a FGB's delicate wings or impale it (e.g., Gillette and Kimbrough 1970), or from other protected sites. In contrast, most of the other katydids observed were found on, and presumably sing from, more exposed sites. Characteristically, the medium-bodied C. wheeleri, C. brevirostris, C. nr brevirostris, D. gigliotosi, M. bradleyi, and the unknown pseudophyllines "a" and "b" are found at night on the upper surfaces of leaves in the forest understory. Similarly, larger bodied species such as A. curvidens, B. tibialis, E. camerani, I. major, and P. tuberosus also occur fully exposed, but on sturdier substrates such as large branches and tree trunks. Last, X. cornea sing in small aggregations in the forest canopy. (The precise locations of singing P. exarmatus, S. fragilis, and M. mortuifolia are not known as members of these three species are relatively rare.)

The short sporadic calls of BCI's forest katydids contrast sharply with the "loud penetrating" calls of Neoconocephalus spp. (Walker and Greenfield 1983; Greenfield 1983, 1988) that are associated with grassy clearings on BCI where FGB do not forage. Nets placed over patches of grass containing these insects and Bucrates capitatus, another regularly calling Copiphorine, captured only frugivorous bats or small aerial insectivore bats, that feed on small flying insects (Belwood, unpublished data).

Call Structure

For the most part, the airborne songs of the Panamanian katydid species studied here consisted of only one or a few "notes" that were produced erratically and sporadically. These occurred either singly (in A. curvidens, B. tibialis, C. brevirostris, E. camerani, I. major, M. bradleyi, P. ex-armatus, P. tuberosus) or in single pairs (in D. gigliotosi, X. cornea). In a few cases, the single or paired notes were repeated up to ten times in a short period of time (in C. nr brevirostris, unknown "b", M. mortuifolia). In only a few cases were calls produced more or less continuously and at regular intervals (C. wheeleri, S. fragilis). In the case of the latter, song duty cycles were still very low (< 5%).

Song carrier frequencies used by the katydids studied were bimodal in distribution. About half used frequencies between 13 and 18 kHz (A. curvidens, B. tibialis, I. pulchripennis, M. bradleyi, M. mortuifolia, unknown "a", unknown "b"), while the others (C. wheeleri, D. gigliotosi, I. major, S. fragilis, X. cornea) used ones between 23 and 27 kHz. Data presented by Morris and Beier (1982) in Costa Rica and by Morris, Klimas and Nickle (in press) in Ecuador indicate that calls from the katydids there fit a similar pattern. Interestingly, the two major frequencies in the calls of C. brevirostris and C. nr brevirostris are in the frequency ranges indicated above.

Whether carrier frequency trends are a function of abiotic factors (e.g., ones that promote optimal signal transmission in a dense forested environment) and/or biotic ones (e.g., ones that could circumvent predator hearing or allow 'acoustical resource partitioning' with other acoustically active animals) is not known. It is noteworthy however, that of the 70 or so katydid species on BCI, members of only six species were taken regularly as prey by the one FGB (Micronycteris hirsuta) that was found to prey heavily on these insects (Belwood this study, Chap. 4). Four of the six (C. wheeleri, D. gigliotosi, I. major, X. cornea), which together constitute 66% by number and 77% by weight of this bat's diet, have carrier frequencies in the 23-27 kHz range. The other two (unknowns "a" and "b") had song carrier frequencies of about 17 kHz. Because M. hirsuta is known to respond to katydid calls (Belwood this study, Chap. 6), this would seem to indicate that the bats have good hearing sensitivities at frequencies much lower than those at which they echolocate (average peak frequency 100.6 ± 10.1 kHz; average range of echolocation call 51.3 ± 7.6 kHz; see Table 5-2). Unfortunately, no data exist on the hearing abilities of these bats.

Insectivorous bats and their prey have long co-evolutionary histories, and bats have influenced the development of anti-predator behavior in moths (Roeder 1967, Spangler 1988), green lacewings (Miller and Olesen 1979), crickets

(Moiseff, Pollack and Hoy 1978), and mantids (Yager and Hoy 1986). In all these cases, insect defenses are based on the ability of the potential prey to hear echolocating bats. Because katydids have ears, use fairly high frequency calls themselves, and are known to have frequency receptors that allow them to perceive calls above about 100kHz, it can also be argued that these insects should be able to perceive echolocating bats. The results of several studies support this idea.

Spangler (1984) reports that some phaneropterines in the southwestern U.S.A. (Insara covilleae, I. elegans) stop singing in the presence of flying bats (species not given). Sales and Pye (1974:121) report similar results for stridulating Conocephalus conocephalus and C. maculatus in Nigeria (bat species also not given). Similarly, McKay (1969, 1970) found auditory neurons in Homorocorhyphus katydids, which were said to be preyed on by bats, that responded to sounds greater than 30 kHz. Whether katydids on BCI can perceive the sounds of echolocating bats is not known, but should be investigated. It is noteworthy, however, that in the laboratory and field, at least some of the area's katydids (A. curvidens, B. tibialis, I. pulchripennis, P. exarmatus, and S. fragilis) continued to sing in the presence of the bats that are attracted to their calls (Belwood this study).

Tremulation

Airborne calls are emitted by male katydids in order to attract females with which to mate. In some cases, these calls also render males susceptible to predation by acoustically orienting predators such as FGB (Belwood this study, Chap. 6). The short sporadic calls of the Latin American pseudophyllines described above appear to lessen some of the risks associated with calling, but should also increase localization difficulties for female katydids that are attracted to males. In apparent response to this, males of many of the pseudophyllines studied here supplemented their shortened calls with tremulation signals. These travel through the substrate, from one individual to another, and are probably not perceived by FGB. Tremulations are analogous to the mating signals that are used by many spiders for mate attraction (Rovner and Barth 1981) and should function well as long distance communication cues since katydids have sensitive vibration receptors (subgenual organs).

Tremulation in katydids appears to be very important. This is supported by the following:

- 1) They are wide spread, at least in the Latin American species that are sympatric with FGB. [N.B., FGB are worldwide in distribution, but compared to bats with other feeding strategies are relatively rare in most geographical areas (Wilson 1973). FGB in the New World (all Phyllotomidae: Phyllostominae) show their greatest diversity and

numbers in Latin America (Hill and Smith 1984).] Tremulations have been reported from katydid species in Costa Rica (Morris 1980; Morris and Beier 1982), Ecuador (Morris, Klimas and Nickle, in press), Panama (this study) and Peru (Belwood, unpublished data). In contrast to other katydids worldwide, which are renowned for their singing abilities, short calls and tremulation appear to be the rule rather than the exception in Latin American forest pseudophyllines.

2) Tremulation is important even in a species that has a high airborne call duty cycle (*I. pulchripennis*). This animal appears to 'prefer' to sing rather than tremulate, as it does the latter only when disturbed (p. 182). Reasons for this are unknown, but are likely to be a function of possible greater energetic costs associated with tremulation. Also, airborne signals probably travel a greater distance and are less directional than substrateborne signals.

3) Tremulations appear to be highly stereotyped, patterned and species specific. Presumably, these help individuals distinguish one species from another and promote reproductive isolation. Patterned signals--i.e., ones that are unique with respect to frequency, duration, regularity, and amplitude and frequency modulation also help katydids distinguish each other from vibrations in vegetation that are caused by abiotic factors (e.g., wind, and leaves and rain that fall on vegetation). It is well known that such

parameters are used by other organisms such as semi-aquatic spiders to discriminate between waves on the water's surface produced by potential prey and those produced by inanimate objects (Bleckmann 1985).

3) In four of the five species in which the temporal aspects of airborne and substrateborne calls were compared, the duty cycle of the latter exceeded that of the former by a factor of at least 2. Substrateborne-to-airborne-call ratios for B. tibialis, A. curvidens, D. gigliotosi, and C. brevirostris were 2.2 to 1, 2.8 to 1, 12.0 to 1, and 95.3 to 1, respectively.

4) Tremulation signals are "rhetorical rather than reciprocal" (Morris 1980:43)--i.e., they are produced whether or not conspecific females are present.

5) Tremulations are also produced by females. Once a female responds to a male with vibration, airborne calling in the male stops and the production of the substrate calls increases dramatically. This occurs at a range of several meters (see B. tibialis, p. 152).

6) At short range, tremulation is incorporated into courtship. This has been described in detail in Copiphora rhinocerus (Morris 1980) and has been observed in B. tibialis, D. gigliotosi, and C. brevirostris in Panama (Belwood, unpublished data) and several unidentified species in Peru (ibid.).

Although tremulation appears to be widespread, much remains to be learned about this phenomenon in Panamanian and other Latin American katydids. For example, how does tremulation help to bring the sexes together for mating? Are both airborne and substrateborne signals necessary for potential mates to find one another? Does vibrotaxis occur? Do females move toward males (in a situation analagous to the response of many katydids to airborne calling songs), or do males move toward females (as occurs under similar conditions in phaneropterine katydids)? Do both sexes move toward one another as occurs in the ephippigerines? Is tremulation restricted only to pseudophyllines and some forest copiphorines? Do females use tremulation to assess male quality (weight)? How important is tremulation in courtship and does it have a role in male-male aggression? These are but a few of the questions pertaining to tremulation that should be addressed with respect to its role in katydid mating behavior.

Similarly, there are many unanswered questions with respect to tremulation and predation. Are the findings presented here a local phenomenon--found only in Latin American katydids--or do similar phenomena occur in pseudophyllines in other geographic areas where FGB are uncommon or absent (e.g., Australian forests)? Some FGB in Africa (Nycteridae) feed on katydids (Fenton 1975, LaVal and LaVal 1980**b**). Do katydids there tremulate? Can wandering spi-

ders or other predatory katydids use these signals to locate tremulating insects? Last, are substrateborne signals truly inaccessible to aerial predators, especially ones that survey their environments with echolocation?

Exactly how FGB locate their prey is not known. Evidence suggests that although they echolocate actively in flight, and while approaching potential prey (Barclay, Fenton et al. 1981), these bats appear to have difficulty distinguishing non-moving prey from the substrates with which they are associated using echolocation alone [Marimuthu and Neuweiler (1987)--M. lyra; Belwood this study, Chap. 6]. Is it possible that echos that return from tremulating insects reveal the presence of the latter to FGB? Whether this is likely to occur should be investigated. It would explain the large proportion of female katydids in the diet of some FGB such as M. hirsuta (Belwood this study, Chap. 4).

Conclusions

Sexual advertisement in Latin American pseudophylline katydids appears to be more complex than that in other katydids. In addition to short, sporadic airborne calls, males of most of the species examined on BCI produce substrateborne signals (tremulations) as a regular part of their long-distance female-attracting advertisement calls. Signalling by females also seems to play a role in pair

formation. In some cases, the substrateborne signals by males greatly exceeds that of airborne ones. Much of this appears related to the presence of acoustically-orienting predators, specifically foliage gleaning bats, that are known to respond to katydid calls, but are not believed to be able to perceive substrateborne signals. The results of this and related studies represent the first example of widespread anti-bat defenses in katydids and open up a new set of possibilities with respect to the study of bat-insect (katydid) interactions.

CHAPTER 8

SUMMARY AND CONCLUSIONS

Bats and insects have long coevolutionary histories. Worldwide, bats are abundant, diverse, and they consume a vast quantity of insects every night as they forage. As a result, they have influenced the development of anti-predator defenses in a variety of insect groups including moths, green lacewings, crickets, and mantids, as already stated. The results of the study described here indicate that this appears to be true in the case of the forest katydids (mainly *Pseudophyllinae*) that are sympatric with foliage gleaning bats in the New World tropics. In that respect, the results presented here open up a new set of possibilities for study of bat-insect interactions and of predator-prey interactions involving predatory phonotaxis.

The results of this study are important for another reason. Although volumes have been written on the physiological and anatomical aspects of acoustics in bats (e.g., Nachtigall 1988) and katydids (e.g., Kalmring and Elsnier 1985), few studies have examined the acoustics of these animals in the context of real ecological settings. Here, an attempt has been made to study the ecology and acoustics of FGB and katydids on Barro Colorado Island in the realm of the other organisms that affect them.

The objectives of this study were to answer three questions:

1) To what extent do FGB in the New World tropics use the airborne calling songs of some katydids to locate these insects as prey?

2) Are FGB important predators of these insect?

3) If the above occur, has predation pressure by FGB influenced calling behavior in katydids.

The results reported here answered these three questions. They indicate that at least four species of bats are indeed capable of locating katydids using the latter's airborne calling songs. Also, at least one of these feeds heavily on these insects. Lastly, members of katydid species that are sympatric with the FGB have calls that are short, sporadic, high-pitched, and difficult for bats to localize. These are supplemented with vibrational signals, which appear not to be sensed by bats as prey-finding cues.

Overall, the trend that emerges is that short, infrequently produced calls and low duty cycles appear to be widespread in the katydids of lowland tropical New World forests. That these are a function of predation rather than another factor, such as habitat-imposed constraints on signal transmission (e.g., Saby and Thorpe 1946, Eyring 1946, Ingard 1953, Morton 1975, Wiley and Richards 1978, Michelsen 1985), is supported by the finding that at least one forest katydid has a long, sustained 'conspicuous' call. However, it is associated with a large spiny

bromeliad that appears to protect it from predation by FGB. A logical next step in the research described in this thesis would be to examine song production in katydids in forested areas in large geographical area where FGB are scarce or absent.

The results of this study also identify a previously unappreciated form of communication in tropical New World katydids--tremulation. This consists of substrateborne signals produced by body vibrations, rather than airborne signals. The importance of tremulation and how it functions to bring the sexes together remains to be demonstrated and should be investigated further.

Last, although it is now known that the echolocation calls of the FGB on BCI are like the calls of other foliage gleaning species, and that these bats respond to katydid calls, the total range of cues used by these animals to locate their prey (e.g. non-calling female katydids) is still not known. How sympatric species that feed on different prey that are gleaned from vegetation distinguish insects from one another also remains to be shown.

The results of this study have raised more questions about the biology and ecology of New World bats and katydids than they have answered. However, they also present an ecologically relevant scenario in which to examine these questions.

APPENDIX

Table A-1.--Weights (in g) of the insects most commonly eaten by the bats in this study. These were used to calculate the biomass of insects eaten. The insects were chilled prior to weighing and their wings and legs were removed. Values for the katydids eaten were taken from the species accounts in Chapter 7. Any other insects consumed were individually weighed.

BODY LENGTH	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50
<hr/>									
HOMOPTERA									
CICADIDAE	0.00	0.09	0.17	0.51	0.63	0.00	2.67	2.70	0.00
OTHERS	0.82	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<hr/>									
ODONATA	0.00	0.00	0.00	0.00	0.00	0.13	0.19	0.26	0.41
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ORTHOPTERA									
GRILLIDAE	0.00	0.00	0.38	0.60	1.10	0.00	0.00	0.00	0.00
BLATTOIDEA	0.00	0.50	0.13	0.19	0.00	0.81	1.41	2.08	3.80
<hr/>									
COLEOPTERA									
SCARABAEIDAE	0.00	0.16	0.26	0.65	0.81	0.00	0.00	0.00	0.00
CERAMBYCIDAE	0.00	0.13	0.27	0.41	0.52	0.00	0.80	0.83	0.00
ELATERIDAE	0.00	0.00	0.17	0.20	0.37	0.00	0.00	0.00	0.00

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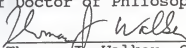
BIOGRAPHICAL SKETCH

Jacqueline Janine Belwood was born in Brussels, Belgium and attended the United Nations International School in New York City. She received a B.Sc. in biology (with first class honours) from Carleton University in Ottawa, Ontario, Canada, and an M.S. in wildlife ecology, and now a Ph.D. in entomology both from the University of Florida, Gainesville.

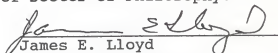
Her research interests focus on the ecology, behavior, and bioacoustics of insectivorous animals (particularly bats) and the insects on which they feed. She is also interested in conservation--particularly that of bats and tropical rainforests.

She likes to travel in search of adventure and interesting animals to study and she loves to dance.

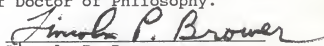
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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December 1988


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